Revision of the genus *Spinosipella* (Bivalvia: Verticordiidae), with descriptions of two new species from Brazil

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ABSTRACT

A revision of the deep-water verticordiid genus *Spinosipella* is provided, based on conchological and anatomical characters. The genus is considered distinct from *Verticordia* (of which it was considered a subgenus) based on the strong ribs, prickly surface, reduction of lunula, relative large size, weakly spiral valve shape, and other characters. The following species are considered in the genus: (1) *Spinosipella agnes* new species, ranging from Florida, USA, to Rio de Janeiro, Brazil, and also including the Porcupine Abyssal Plain in the North Atlantic; (2) *S. tinga* new species, occurring from Rio de Janeiro to Rio Grande do Sul, Brazil; (3) *S. acuticostata* (Philippi, 1844), a Pliocene fossil from southern Italy; (4) *S. deshayesiana* (Fischer, 1862), from south and central Indo-Pacific (*S. ericia* Hedley, 1911, the type species of the genus, was revealed to be a new synonym of *S. deshayesiana*); and (5) *S. costeminens* (Poutiers, 1981), from the tropical west Pacific. The five species differ mainly in conchological details of the number and size of ribs, of the prickly sculpture, shape of the shell, of the hinge and the degree of convexity. Anatomical description is also provided for the two Pacific species, which differ among themselves mainly by the size of the pair of renal folds. From the standpoint of anatomical characters, the more significant are: the wide lithodesma; the elongation of the auricles, crossing the roof of pallial cavity; a tall digital fold in posterior region of supraseptal chamber; the low but wide palps; the muscular, gizzard-like stomach; the complete separation of both constituents of the hermaphroditic gonad (a ventro-posterior testicle and a centro-dorsal ovary), and a complete fusion of the visceral ganglia.

Additional Keywords: Mollusca, Anomalodesmata, Septibranchia

INTRODUCTION

The Verticordiidae is a family of septibranch bivalves comprised of carnivorous and mostly deep-water species. They are typically small (less than 10 mm) but some species reach 30–40 mm. They are mostly radially sculptured and usually have nacreous inner surface.

The genus *Spinosipella* Iredale, 1930 (type *Verticordia ericia* Hedley, 1911, by original designation) is usually considered a subgenus of *Verticordia* Sowerby, 1844 (e.g., Thiele, 1934; Moore, 1969; Abbott and Dance, 1983). The genus encompasses species with shell having prickly outer surface, lunule very reduced, thick walls, and generally larger size (up to 30 mm). In addition to the type species, *S. ericia*, three other species are currently included in this genus, *S. acuticostata* (Philippi, 1844), from Atlantic and Mediterranean (middle Tertiary to Recent); *S. deshayesiana* (P. Fischer, 1862a) and *S. costeminens* (Poutiers, 1981), from Indo-Pacific. Some authors have considered *S. deshayesiana* as an Indo-Pacific occurrence of *S. acuticostata* (e.g., Nobre, 1936; Crozier, 1966; Rosenberg, 2005).

Examination of worldwide samples, with an emphasis on the Western Atlantic, showed that two species actually exist in the Atlantic. Both are separate from the fossil S. acuticostata. In addition, it was possible to reorganize the Indo-Pacific species, mainly because of the abundant material deposited at the Muséum national d'Histoire naturelle, Paris (MNHN), which results from several expeditions. A revision of the taxonomy and a necessary re-definition of taxa are provided in this paper, as part of a larger project revising Western Atlantic mollusk taxonomy, based on morphology.

MATERIALS AND METHODS

A detailed list of the material examined follows each species description. Specimens generally belong to museum collections. Most material consists of shells examined under a stereomicroscope. Some few Pacific samples have preserved soft parts in 70% ETOH. They were dissected by standard techniques, under stereomicroscope, with specimen immerse in alcohol. All dissecting steps were digitally photographed; all drawings were made with the aid of a camera lucida. In the case of the material examined of *Spinosipella deshayesiana* and

S. costeminens, as the quantity of examined lots is very large, mainly thorugh courtesy of staff at MNHN (Paris), the list only contains the country and the quantity of specimens. The full list of examined lots of these specimens is being published elsewhere, in a complementary paper (Simone and Cunha, in press).

Abbreviations used in figures are: am, anterior adductor muscle; **an,** anus; **au,** auricle; **bs,** byssus; **by,** byssal gland or furrow; **cc,** cerebral commissure; **ce,** cerebral ganglion; **cj,** connective tissue; **cm,** circular muscle layer; **co,** cerebro-visceral connective; **cr,** crustacean inside stomach; **cv,** ctenidial (efferent) vein; **dd,** ducts to digestive diverticulae; **dg,** digestive diverticula; **es,** esophagus; **fa,** foot aperture of mantle; **fm,** posterior foot retractor muscle; **fr,** anterior foot retractor muscle; **ft,** foot; **ga,** genital aperture; **ge,** gastric epithelium; **gi,** gill; **he,** hemocoel; **ic,** infra-septal chamber; **in,** intestine; **ki,** kidney; **lm,** lateral muscle; **lo,** longitudinal muscle layer; **lt,** lithodesma; **mb,** mantle border; **mf,** fused mantle edge; **mg,** radial mantle gland; **mo,** mouth; **mp,** mantle tentacle; **ms,** mantle muscles of incurrent siphon; **mt,** mantle; **mu,** muscular tissue; **ne,** nephropore; **nv,** nerve; **oy,** ovary; **pa,** posterior adductor muscle; **pc,** pericardium; **pg,** pedal ganglia; **pi,** papilla of excurrent chamber roof; **pm,** pallial muscles; **pp,** palp; **rs,** renal fold; **rt,** rectum; **se,** excurrent siphon; **sh,** shell; **si,** incurrent siphon; **sm,** septum muscle; **sp,** septum; **ss,** style sac; **st,** stomach; **su,** supra-septal chamber; **sy,** crystalline style; **ts,** testis; **um,** shell umbo; **ve,** ventricle; **vg,** visceral ganglia; **vm,** visceral mass.

Abbreviations of institutions: AMS, Australian Museum at Sydney, Australia; EGC, Emilio Garcia collection; FMNH, Florida Museum of Natural History, Florida, USA; HGLC, Harry G. Lee collection; INVEMAR-MHNMC, project of Museo de Historia Natural Marina de Colombia; MHNMC, Museo de Historia Natural Marina de Colombia (Programa de Biodiversidad y Ecosistemas Marinos); MNHN, Muséum national d'Histoire naturelle, Paris, France; MZSP, Museu de Zoologia da Universidade de São Paulo, Brazil; RLPC, Rafael La Perna collection (Universitá di Bali, Italy).

Specimens from other verticordiid species were also examined for comparative purposes. This material includes:

Haliris fischeriana Dall, 1881:

UNITED STATES OF AMERICA. Florida, Fowey Light, 130 m depth, MZSP 19934, 2 valves (R.V. Eolis sta. 184). BRAZIL. Rio de Janeiro; 22°34′ S, 40°29′ W, 213 m depth, MZSP 18751, 1 valve (on Laminarias, W. Besnard col. est. IX). Rio Grande do Sul; 30°42′ S, 49°03′ W, 182–186 m depth, MZSP 18750, 5 valves (21 Aug. 1972); 32°55′ S, 50°34′ W, 99 m depth, UFRG 1688, 1 shell and 10 valves (sta. 45, 6839 dredge, 04/iv/1998).

Euciroa sp.:

BRAZIL. Rio Grande do Sul, off Tramandaí, 30°42′ S, 49°03′ W, 182–186 m, MZSP 18750, 5 valves (R/V W. Besnard, GEDIP sta. 1856, 21 Aug. 1972). MADAGASCAR. 600 m depth, EGC 23588, 1 shell. MOZAMBIQUE. off Morondava, Channel Madagascar, 600–800 m depth, MZSP 61816, 3 shells (Trawled by local fisherman, May 2002).

Euciroa elegantissima (Dall, 1881).

UNITED STATES OF AMERICA. Florida, 27°16′ N, 84°58.99′ W, 457 m depth, EGC 13005, 6 valves (dredged, R/V Pelican), 24°09′ N, 82°31′ W, about 64.3 km off Southwest of Key West, 549 m depth, EGC 23688, 1 shell (R/V Oregon II col, cruise #45, sta. 13362); Monroe Co. Straits of Florida, 549 m depth, FMNH 209892, 1 shell (Frank Lyman col.), 24°15.1′ N, 82°11.71′ W, 525 m depth, FMNH 164794, 1 valve (G.H. Burgess, et. al. GHB-90-8, 23 Apr. 1990). COLOMBIA. Santa Marta, Cerro de Punta Betin, A.A. 1016, (MHNMC INVEMAR), MHNMC 2782, 3 valves, MHNMC 2781, 1 valve.

SYSTEMATICS

Genus *Spinosipella* Iredale, 1930

Iphigenia Costa, 1850: 398 (type species by original designation *Hippagus acuticostatus* Philippi, 1844) (pre-occupied) (non Schumacher, 1817).

Spinosipella Iredale, 1930: 388 (type species by original designation *Verticordia ericia* Hedley, 1911); Poutier and Bernard, 1995: 142.

Verticordia (Spinosipella): Thiele, 1934: 1428; Moore, 1969: 855.

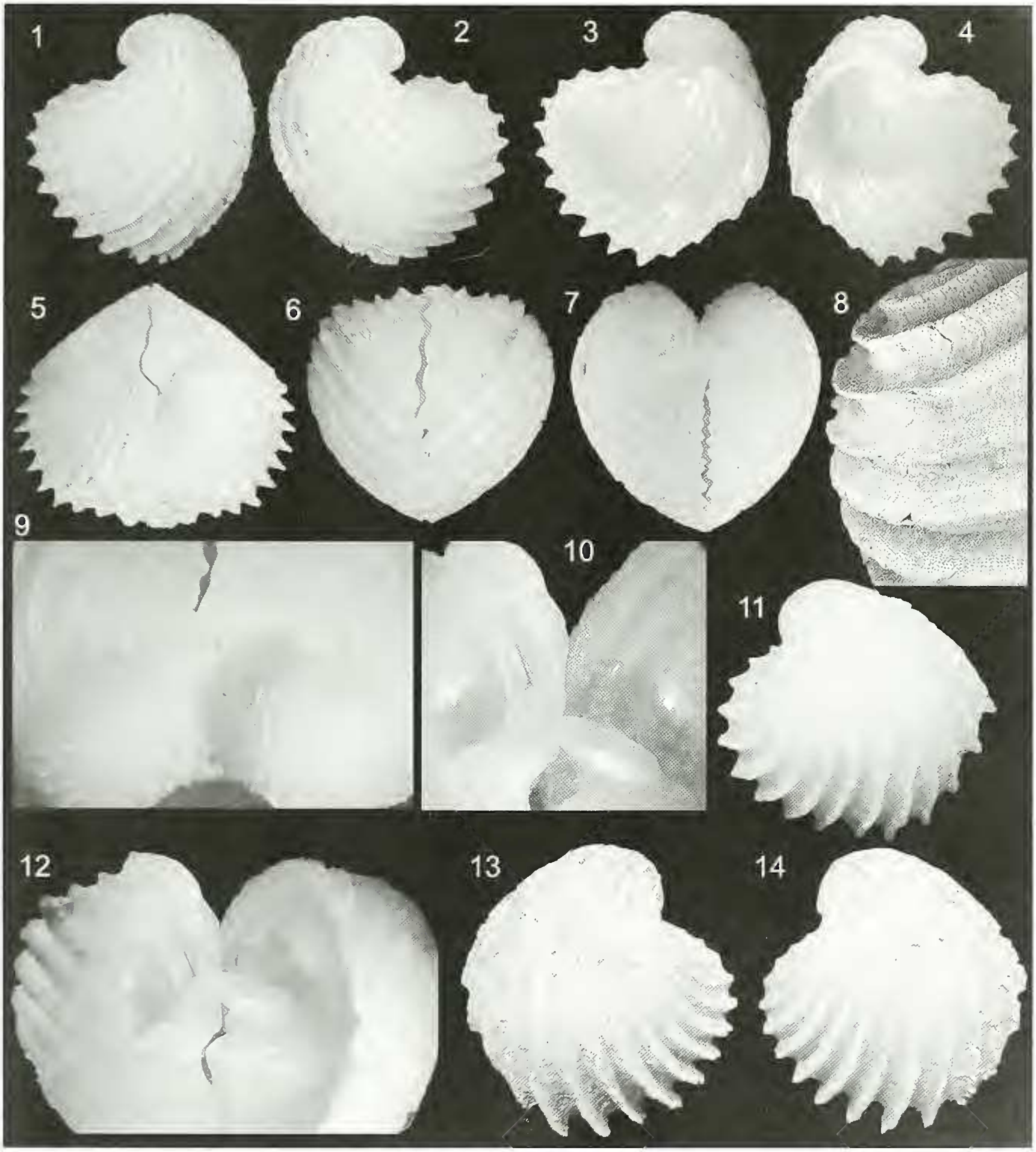
Diagnosis: Shell relatively large, obese, with spiral valves. Surface prickly including on radial ribs. Radial ribs tall, extending beyond shell margin. Lunula very reduced.

Description: Shell: From small to medium size (up to 30 mm). Width/length ratio usually about 1. Color opaque-whitish. Sculptured by strong and tall radial, weakly curved ribs, triangular in section, bulging weakly beyond shell edge, alternating in both valves. Surface spiny, constituted by uniform sized, very small bulbs, covering almost entire outer surface. Lunula very reduced. Umbo projected, weakly spiral. Right valve with single tall, pointed and broad cardinal tooth. Left valve with low, broad tooth (posterior to tooth of right valve), and plane cardinal concavity as socket of tooth of right valve. Ligament just anterior to anterior hinge tooth, inserted at some distance from median line, in approximately middle way between hinge medial edge and umbonal cavity (Figures 10, 12). Lithodesma wide, curve, occupying about 0.25 of hinge length, possessing a pair of lateral ligamental articulations (Figures 93, 96–105).

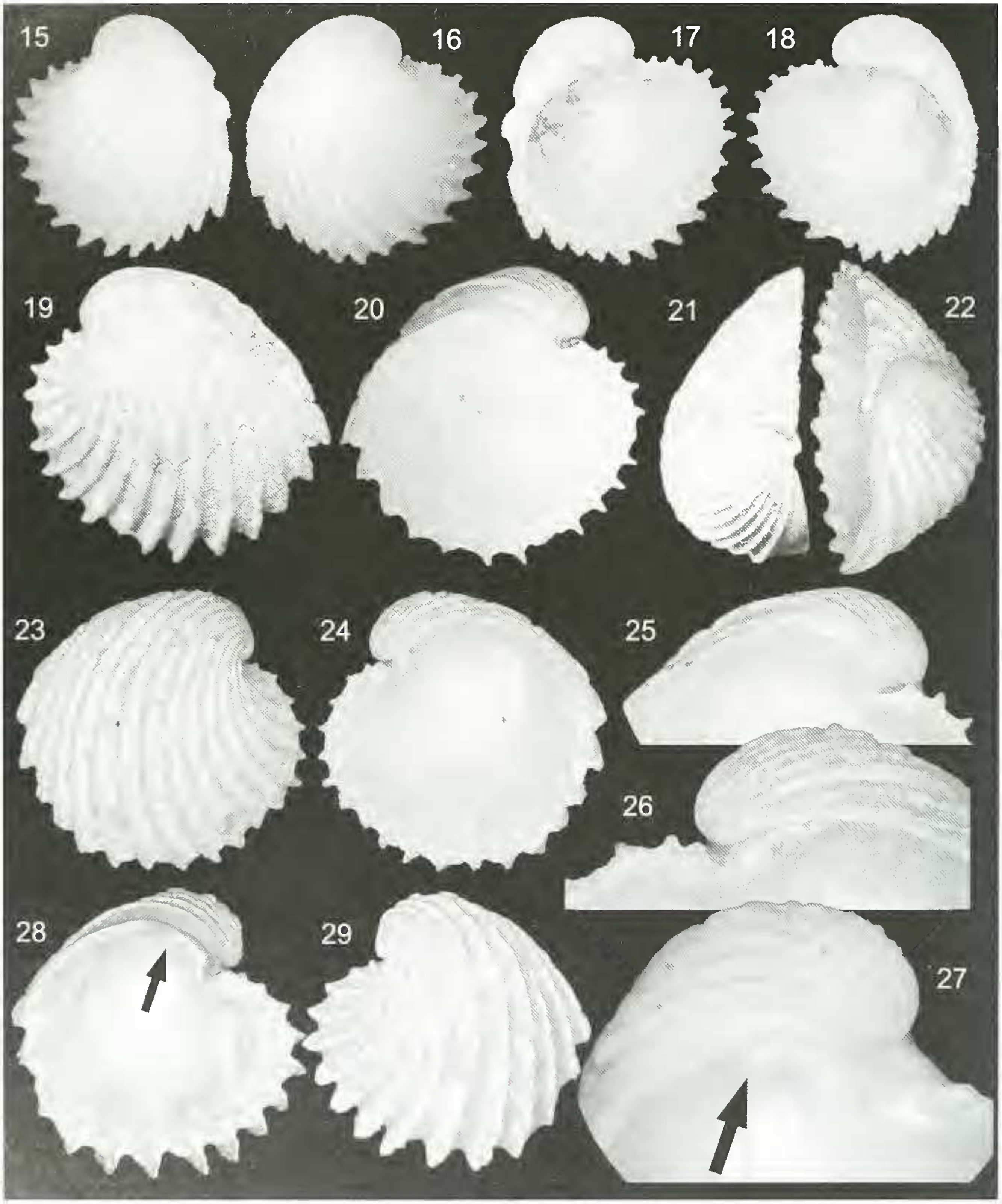
List of Included Taxa: *S. acuticostata* (Philippi, 1844); *S. agnes* new species; *S. costeminens* (Poutiers, 1981); *S. deshayesiana* (P. Fischer, 1862a) [=*S. ericia* (Henley, 1911)]; *S. tinga* new species.

Spinosipella agnes new species
(Figures 1–18, 27–29, 31, 55)

Verticordia acuticostata.—Nobre, 1936: 303–304; 1938: 769–770; Abbott, 1974: 563; Abbott and Dance, 1983: 375



Figures 1–14. *Spinosipella agnes* new species. Shells. **1–10.** Holotype (length 23.2 mm) shell. **1.** Left valve, outer view. **2.** Right valve. **3.** Right valve, inner view; **4.** Left valve, inner view. **5.** Dorsal view. **6.** Posterior view. **7.** Anterior view. **8.** Detail of shell surface in SEM, middle region of right valve. **9.** Detail of inter-umbonal region, dorsal view. **10.** Hinge, ventral-inner view. **11–14.** Paratypes. **11.** HGLC, from Florida, left valve, outer view; 11 mm. **12.** Same, ventral view, valves opened for showing whole view of hinge. **13–14.** EGC 17419, from Colombia, outer view of right and left valves; 18 mm.



Figures 15–29. *Spinosipella* new species. Shells. **15–18.** *S. agnes* paratype AMNH 162803, Florida, specimen with remains of soft parts; 14.8 mm. **19–26.** *S. tinga* type specimens. **19–21.** Holotype, left valve, outer, inner and dorsal views; 16.9 mm. **22–24.** Paratype MORG 18085, right valve, dorsal, outer and inner views; 10.1 mm. **25.** Holotype, detail of hinge, left valve. **26.** Paratype MORG 18085, right valve, detail of hinge. **27–29.** *S. agnes*. **27.** Holotype, left valve, detail of hinge; arrow indicating well-developed posterior cardinal tooth. **28–29.** Paratype INV MOL 2943, from Colombia, a specimen of equivalent size of main types of *S. tinga* for showing major differences (compare with Figures 19–20); inner and outer views; 17.0 mm; note developed posterior cardinal toot of hinge (arrow), fewer, taller and more spaced ribs and more projected ribs at edges.

(fig.); van Aartsen, 1992: 45; Poppe and Goto, 1993: 139; ?McLean and Geiger, 1998: 27, 109 (fig.); Salas, 1996: 46; Rosenberg, 2005 (part) (non Philippi, 1844).

Verticordia deshayesiana.—Rosenberg, 2005 (part) (in synonymy) (non Fischer, 1862a).

Type Material: HOLOTYPE, MZSP 36917; BRAZIL. Rio de Janeiro, off Cabo Frio, 23°41′ S, 41°03′ W, 750–800 m depth (o.t.). PARATYPES. UNITED STATES OF AMERICA. Florida; Off Cape Canaveral, 903 m depth, USNM 64039, 1 right valve; SE of Sand Key, AMNH 248458, 4 shells (Jan. 1970, J. M. Bijur Collection), AMNH 248459, 2 shells (Jun. 1970, J. M. Bijur Collection); Monroe County, S.E. Sand Key, 270 m depth, HGLC, 2 shells, FMNH 154594, 1 specimen (dredged, Jerry Phelps col., Jun. 1970); 120.6 km east of Daytona, 29°17′ N, 79°27′ W, 878 m depth, USNM 810590, 1 shell and 1 left valve (R/V. OREGON, sta. 6690, 9 May 1967); Marquesas Key, 24°15′ N, 82°13′ W, 278–419 m depth. 1 left, USNM 810889, 1 right valve (R/V. Blake, A. Agassiz 1877–1878). COLOMBIA. off Cartagena, 10°28′ N, 75°42′ W, 280 m, MHNMC 2203, 1 valve (E-47), 10°31′ N, 75°37′ W, 309 m, MHNMC 2775, 1 valve (E-141), Palomino, Dibulla, 11°29′ N, 73°27′ W, 476 m, MHNMC 3104, 4 valves, (E-21), Guajira, Bahía Honda, 12°31′ N, 72°8′ W, 452 m, MHNMC 2943, 1 shell (E-12), Guajira Peninsula, 12°30′ N, 72°08′ W, 470 m depth, EGC 17419, 1 shell; Cabo de la Vela, 12°19′ N, 72°42′ W, 464 m, MHNMC 3087, 2 valves (E-19), Islas del Rosario, 10°10′ N, 76°01′ W, 510 m, MHNMC 2208, 2 valves (E-78). BRAZIL. Rio Grande do Norte; 206 m depth, MZSP 84627, 1 shell (Sta. D-22, 10 Nov. 2001); Pernambuco; 690 m depth, MZSP 84628, 1 shell (Sta. D-11).

Diagnosis: Shell with 15–17 radial ribs; smooth pre-umbonal region wide (about 0.25 of shell length); prickly sculpture chaotically organized. Width/length ratio in each valve approximately 0.57. Posterior cardinal tooth of left valve hinge well developed; main cardinal tooth of left valve relatively low and cylindrical; main cardinal tooth of right valve tall (about 0.2 of valve width) and pointed.

Description: SHELL: Up to 22 mm, equivalve, inflated, each valve symmetrically and weakly spiral (1 whorl) (Figures 7, 9). Color white. Degree of convexity (width/length) in each valve approximately 0.57. Outer surface spiny, opaque forming an irregular mosaic (Figures 8, 9). Umbones located in middle region of dorsal surface, spiral, high, divergent. separated from each other at about ⅓ of shell width (Figures 1–4, 13–18, 55). Sculptured by strong, uniform, arched, radial ribs, from 15 to 17 in each valve. Posterior edge about twice as wide as anterior edge. Between umbo and anterior edge a concavity bearing transversal ribs, slightly wider than ribs of remaining region (Figures 5, 7, 9). Pre-umbonal region smooth, narrow, 0.2 of shell length (Figures 5, 7, 9). Anterior, ventral and posterior edges forming zigzag (Figures 3, 4); tips of this zigzag coinciding with tips of each rib, tips encasing in concavity of opposite valve (Figures 1, 2, 11, 13–16). Inner surface iridescent, whitish, glossy; including hinge (Figures 3, 4, 10, 12, 17, 18). Hinge with a large cardinal tooth in right valve, stubby, tall (about 20% of valve width), broadly pointed, weakly curved forwards (Figures 3, 10, 12, 18), circular in section; correspondent socket in left valve shallow, restrict to dorsal surface; this socket flanked by small tooth in each side, anterior smaller and lower than posterior (Figures 4, 10, 12, 17, 27–28 [arrow]). Ligament just anterior to anterior hinge tooth, inserted at some distance from median line (Figures 10, 12), approximately midway between hinge medial edge and umbonal cavity. Scars of adductor muscles shallow (Figures 3, 4, 17, 18, 28); anterior scar elliptical (longer dorso-ventrally), located close to anterior edge, area about ⅟₁₅ of inner surface of valve; posterior scar circular, about 0.33 larger than anterior scar, located close to posterior shell edge. Pallial line continuous, located at wide distance from shell edge, about 0.33 of distance between ventral and umbonal height.

Measurements (Length, height, width, in mm): Holotype: 20.1 by 23.2 by 22.2; EGC 17419: 15.6 by 15.5 by 15.5.

Geographic Distribution: Florida, USA, to Rio de Janeiro, Brazil.

Habitat: Muddy bottoms, 270–900 m.

Material Examined: Types. BARBADOS. USNM 63200, 3 valves (Blake Coll., sta. 100). CUBA. Havana; Gulf of Mexico, 419 m depth, USNM 63201, 3 right, 4 left valves (Blake Coll., sta. 5). PORTUGAL. Porcupine Bank; USNM 63204, 2 right valves (Jeffreys Coll., Porcupine Exp. 1870). UNITED STATES OF AMERICA. Florida; Gulf of Mexico, off Cape San Blas, 309 m depth, USNM 323871, 1 left, 1 right valve (sta. 2400); 120.6 km east of Daytona, 29°17′ N, 79°27′ W, 878 m depth, USNM 810590, 1 shell and 1 left valve. BRAZIL. Espírito Santo (R/V MARION-DUFRESNE MD55, May 1987); off Conceição da Barra, 18°59′ S, 37°50′ W, 637 m depth, MNHN, 10 valves (sta. CB76); off Pontal da Regência, 19°34′ S, 38°55′ W, 340–360 m depth, MNHN 1 valve (sta. CB92).

Etymology: The specific epithet refers from the Greek *agnes*, meaning pure, an allusion to the whitish color of the shell.

Remarks: The above listed examined material that was not designed as types are normally lots with eroded specimens, or sometimes they have aberrant characters. This is the case of the MNHN material collected off north coast of Espírito Santo, Brazil. They actually are free valves that resemble the Pacific species *Spinisopella costeminens*, in having a weakly larger radial thread between middle and posterior thirds, and in lacking anterior tooth in hinge. As they can represent another species, they are not designed as types; on the other hand, the material is not sufficiently well-preserved for further analysis. Because of they can only represent an extreme of variation of the *S. agnes*, they are listed as additional examined material of this species.

Spinosipella tinga new species
(Figures 19–26, 30, 32)

Verticordia acuticostata: Marini, 1974: 242, figs. 5, 6 (non Philippi, 1844).
Verticordia (Haliris) acuticostata: Rios, 1975: 262, pl. 85., fig. 1261; 1985: 282, pl. 99, fig. 1391; 1994: 304, pl. 104, figs. 1489 (non Philippi, 1844).
Verticordia deshayesiana: Marini, 1974: 242 (in synonymy); Rios, 1975: 262; 1985: 282; 1994: 304 (in synonymy); Rosenberg, 2005 (part) (in synonymy) (non Fischer, 1862a).

Diagnosis: Shell with 17–18 radial ribs; smooth pre-umbonal region very narrow (less that ⅕ of shell length). Width/length ratio in each valve approximately 0.47. Posterior cardinal tooth of left valve hinge absent; main cardinal tooth of left valve low and cylindrical; main cardinal tooth of right valve lower (about 10% of valve width) and rounded.

Description: SHELL: Up to 11 mm, equivalve, inflated, both valves weakly spiral (1 whorl) (Figures 21, 22). Color white. Degree of convexity (width/length) in each valve approximately 0.47. Umbones located in middle region of dorsal surface (Figures 19, 20, 23, 24); umbones weakly spiraled, somewhat high, divergent, separated from each other. Sculpture of strong, uniform, arched, radial ribs, 17–18 in each valve. Outer surface opaque, covered by a mosaic of small, blunt, loosely aligned spines parallel to radial ribs (Figure 32). Anterior edge almost same size as posterior edge. A concavity bearing transversal ribs of same width as remaining ribs between umbo and posterior edge (Figures 21, 22, 30). Anterior, ventral, and posterior edges rounded, tips of ribs prominent (Figures 19, 20, 23, 24), fitting with concavity in opposite valve. Inner surface iridescent, whitish, glossy, including hinge. Hinge with a somewhat large cardinal tooth in right valve (Figures 20, 25); cardinal tooth stubby, tip rounded, flat in cross-section, tooth length about 10% of valve width; correspondent socket in left valve shallow, restricted to dorsal surface; this socket flanked by small, low, posterior tooth (no anterior tooth) (Figures 24, 26). Ligament just anterior to anterior hinge tooth, inserted at some distance from midline, approximately midway between hinge medial edge and umbonal cavity. Scars of adductor muscles shallow (Figures 20, 24); anterior scar elliptical (longer dorso-ventrally), located close to anterior edge, area about 1/15 of inner surface of valve; posterior scar circular, about ⅓ larger than anterior scar, located close to posterior shell edge. Pallial line with a very weak pallial sinus, located at wide distance from shell edge, about ⅓ of distance between ventral and umbonal height.

Measurements (respectively length, height, width, in mm): Holotype: 16.9 × 15.3 × 9.6 (single valve); MZSP 18752: Paratype #1, 8.6 × 8.6 × 4.1 (1 valve); Paratype #2, 11.9 × 11.4 × 5.4 (1 valve); MZSP 18753: 9.5 × 9.6 × 4.8 (1 valve).

Type Material: Holotype, MZSP 19345, 1 valve, from type locality (R/V W. BESNARD, GEPID Est. 458, 9 Dec. 1968. Paratypes, Rio de Janeiro, Cabo de São Tomé, 31°08′ S, 49°31′ W, 182–253 m, 1 valve, MZSP 18752 (R/V W. BESNARD, GEDIP st. 1858, 6 Aug. 1972); 22°34′ S, 40°29′ W, 213 m, 1 valve, MZSP 18753; (R/V W. BESNARD, st. IX, 11 Feb.1969), 100 m, 2 valves, MORG 18085 (R/V ALMIRANTE SALDANHA, Mar. 1972), off Solidão, 240 m, 2 valves, MORG 31888 (R/V ATLÂNTICO SUL, Exp. Coltro, 14 Oct.1993).

Type Locality: BRAZIL. Rio Grande do Sul, off Albardão, 33°29′ S, 50°44′ W, 200 m, muddy bottom.

Geographic Distribution: Brazil, from Rio de Janeiro to Rio Grande do Sul.

Etymology: The specific epithet refers to the color white of the shell, from the Tupy language: *tinga*.

Spinosipella acuticostata (Philippi, 1844)
(Figures 33–40)

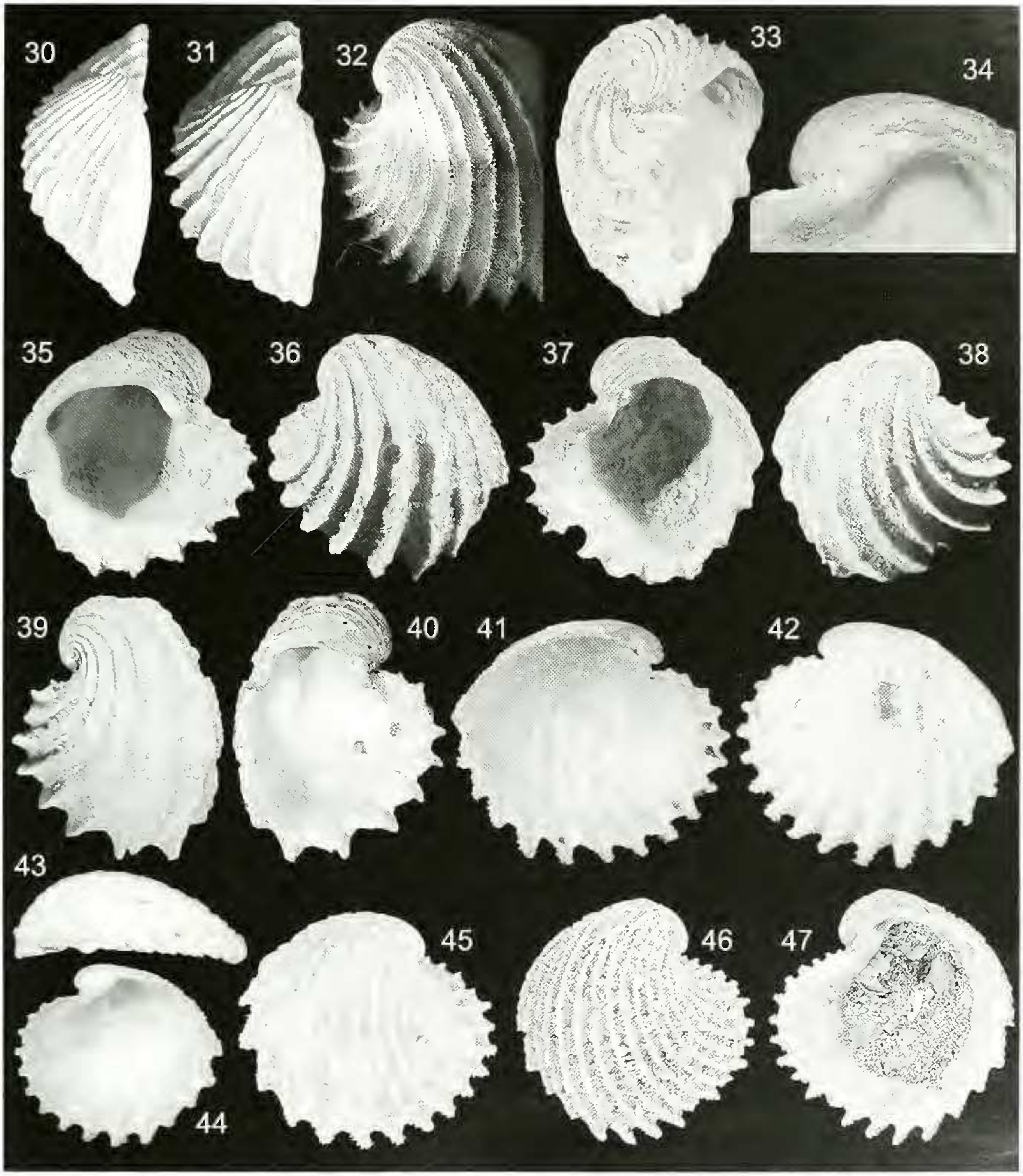
Hippagus acuticostatus Philippi, 1844: 42 (pl. 14, fig. 19) [fossil in Lamati valley, Calabria, Italy].
Verticordia acuticostata: Micali and Villari, 1991: 353.
Spinosipella acuticostata: Poutiers and Bernard, 1995: 143, 155.

Diagnosis: Shell with 12–13 radial ribs; pre-umbonal region narrow, smooth; posterior cardinal tooth of left valve hinge shallow or absent; main cardinal tooth of left valve longer and flat (Figures 35, 40); main cardinal tooth of right valve shallower (Figures 34, 37) (about 10% of valve width).

Description: SHELL: Up to 24 mm; width/length ratio approximately 1 (Figures 36–38) to 1.5 (Figures 39, 40). Degree of convexity (width/length) in each valve approximately 0.55. Outer surface spiny, opaque, spines forming radially aligned mosaic parallel to ribs (Figures 36, 38, 39). Sculpture of strong, uniform, arched, radial ribs, 12–13 in each valve. Posterior edge about twice as broad as anterior edge. A concavity bearing transversal ribs weakly broader than ribs of remaining region between umbo and anterior edge (Figures 35, 39); pre-umbonal region narrow, smoooth (Figure 33), about 10% of shell length. Anterior, ventral, and posterior edges forming zigzag (Figures 35, 37, 40). Hinge with a large cardinal tooth in right valve, stubby, tall (about 10% of valve width), broadly pointed, weakly curved anteriorly (Figures 34, 37), circular in section; correspondent socket in left valve shallow, restricted to dorsal surface; this socket sometimes flanked by small tooth in each side, anterior absent or very weak (Figures 35, 40).

Measurements (respectively length, height, width, in mm): RLPC #1: 11.4 × 14.5 × 6.6 (valve); #2: 10.0 × 9.8 × 4.7 (valve).

Geographic Distribution: Mediterranean. Pliocene fossil from south Italy (Calabria and Sicily).



Figures 30–47. *Spinosipella* species. Shells. **30.** *S. tinga*, Holotype, left valve, dorsal view. **31.** *S. agnes*, Paratype INV-MOL 2943, from Colombia, a specimen of equivalent size of Holotype of *S. tinga* for showing major differences (compare with Figure 30); dorsal view: 17.0 mm: note higher convexity, fewer, taller and more spaced ribs. **32.** *S. tinga*, left valve, SEM of Holotype, showing prickly sculpture. **33–40.** *S. acuticostata*. **33–38.** Pliocene fossil from Messina, Italy, USNM 63202. **33**, Specimen 2, dorsal-slightly anterior view. **34.** Specimen 3, right valve, detail of hinge. **35–36.** Specimen I, left valve, inner and outer views; 13.5 mm. **37–38.** Specimen 2, right valve, inner and outer views, hinge broken; 12.2 mm. **39–40.** RLPC, from Rometta, Italy, left valve, specimen with long shape: 19.0 mm. **41–47.** *S. deshayesiana*. **41–43.** Paratype 1 of *S. ericia* AMS 032068, left valve, inner, outer and dorsal views; 3.5 mm. **44.** Paratype 2, right valve, inner view; 2.6 mm. **45** Type specimen of *S. japonica* ANSP 49639, right valve; 5.2 mm **46–47.** ANSP 292986 (from India), right valve, outer and inner views; 10.5 mm.

Paleohabitat: Middle and upper Pliocene beds of bathyal environments.

Material Examined: ITALY. Sicily, Messina, 38°11′ N, 15°34′ E, Seguenza, USNM 63202, 2 left, 2 right valves. Middle Pliocene outcrops at Rometta, 4 valves, RLPC.

Spinosipella deshayesiana (Fischer, 1862)
(Figures 41–54, 66, 67, 72–82, 93–102)

Verticordia Deshayesiana Fischer, 1862a: 35–36 (pl. 5, fig. 10–11) [China Sea].
Verticordia japonica A. Adams, 1862: 224.
Verticordia ericia Hedley, 1911: 96; Prezant, 1998: 421 (fig. 9.16A).
Spinosipella deshayesiana.—Poutiers and Bernard, 1995: 110–112, 143, 159, 161 (figs. 7–9).
Spinisopella ericia.—Poutiers and Bernard, 1995: 143, 159.
Verticordia acuticostata.—McLean and Geiger, 1998: 109 (non Philippi, 1844).

Diagnosis: Shell with 16–19 radial ribs uniformly distributed, closely packed; pre-umbonal region narrow, smooth. Each rib bearing well-developed crests with small, prickly granules. Posterior cardinal tooth of left valve hinge absent; main cardinal tooth of left valve low and flat, with insertion of anterior valve edge approximately in middle region of this tooth; main cardinal tooth of right valve high (about 10% of valve width) and pointed.

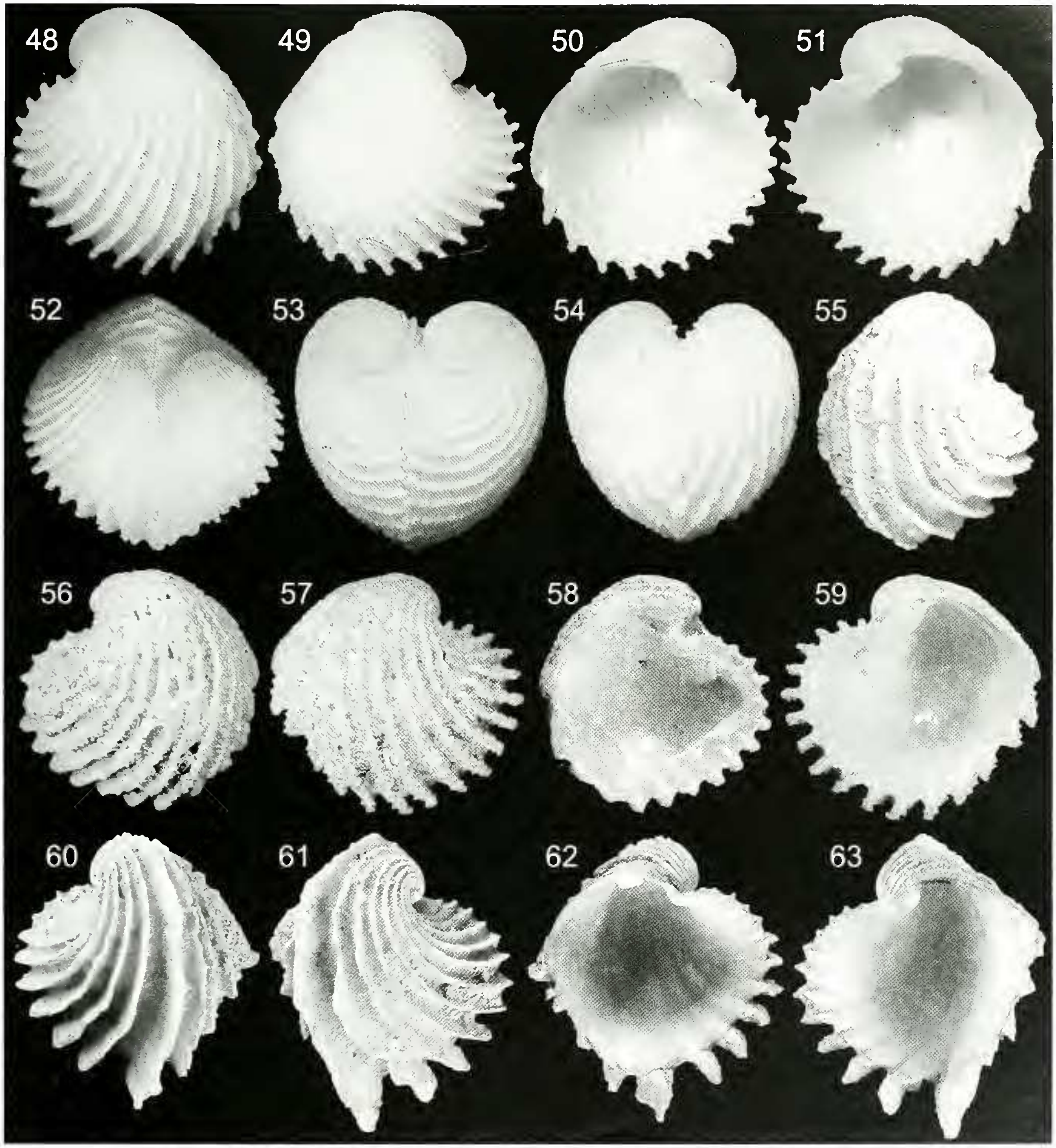
Description: SHELL: Up to 18 mm. Color white. Degree of convexity (width/length) in each valve approximately 0.57. Outer surface spiny, spines organized somewhat radially, parallel to ribs; each rib with well-developed crests with small, prickly granules (Figures 42, 45, 46, 48–54). Sculpture of strong, uniform, arched, radial ribs, 16–19 in each valve (Figures 42, 45, 46, 50), somewhat closely packed. Posterior edge about twice broader than anterior edge. A concavity bearing transversal ribs similar to ribs of remaining region present between umbo and anterior edge (Figures 43, 53); pre-umbonal region narrow, smooth, about 10% of shell length (Figures 43, 53). Anterior, ventral, and posterior edges forming zigzag (Figures 42, 44, 47, 50, 51, 59, 67, 100), with tips projected, longer, and narrower. Hinge with a large cardinal tooth in right valve, stubby, tall (about 10% of valve width), broadly pointed, somewhat flat (Figures 44, 47, 51, 59, 67); correspondent socket in left valve shallow, restrict to dorsal surface; this socket flanked by small posterior tooth, with insertion of anterior valve edge approximately in middle region of this tooth (Figures 41, 50), anterior tooth absent (Figures 41, 50).

LITHODESMA (Figures 93, 96–99): Saddle-shaped, hemi-cylindrical. Dorsal surface concave (Figures 97–98), flanking ventral surface of hinge, along ¼ of hinge length; located just posterior to teeth. Left and right edges straight, turned upwards and medially, connected with valves by dark-brown ligament inside umbonal cavity closer to hinge inner edge (Figures 100–102). Outer surface convex, covering dorsal-middle, inter-umbonal region of visceral mass (Figure 75). Anterior and posterior edges concave; anterior edge slightly deeper and with tenuous slope. Both edges covered by opaque, yellowish periostracum (Figures 96, 101, 102). Lithodesma thickness equivalent to that of shell.

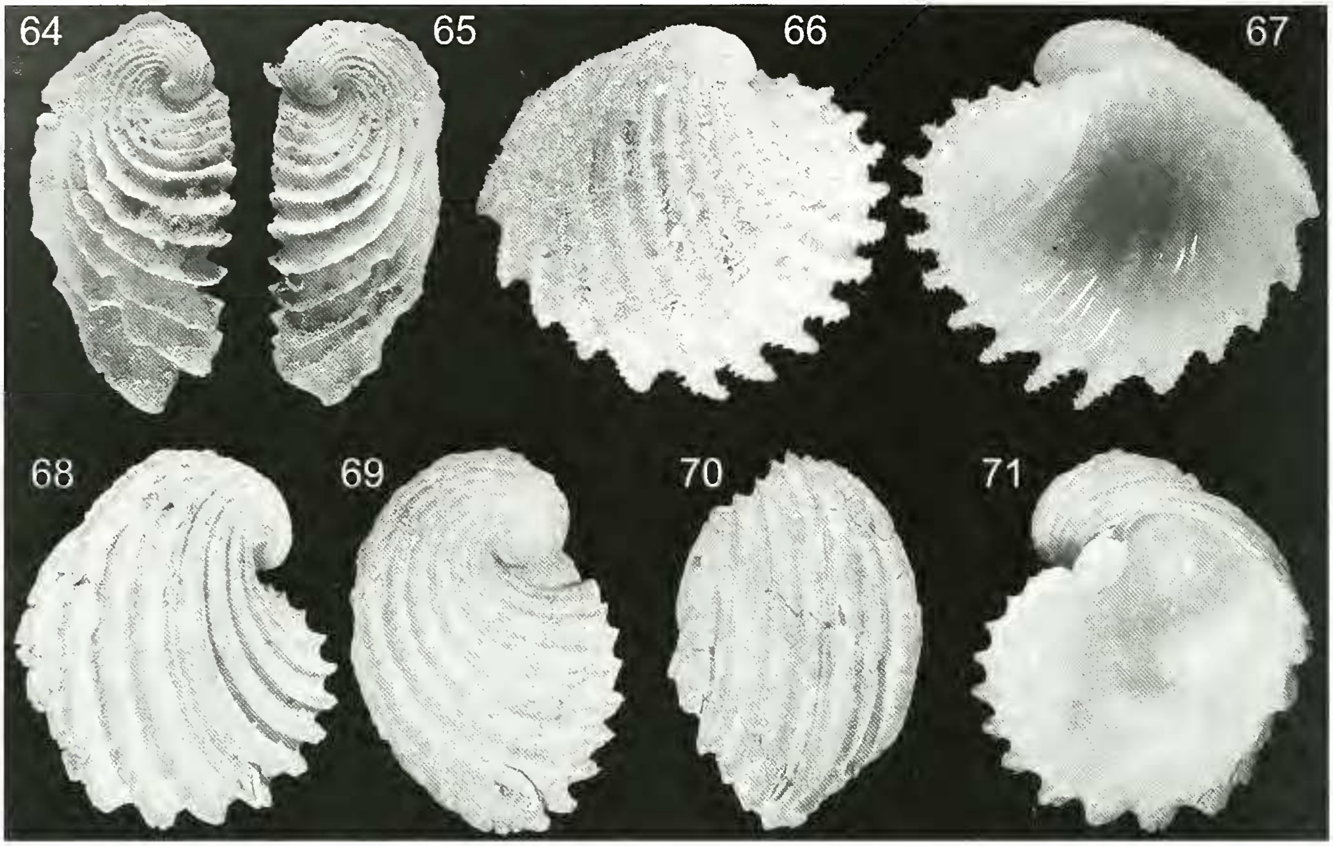
MAJOR MUSCLES (FIGURES 72–75, 77, 78, 80, 91, 92): Both adductor muscles similar in size and position (Figures 72–75), near valve edges; insertion size equivalent to 1/20 of valves inner surface each; approximately two times taller than wide; outer length about half of inner length, with insertion in valves greatly oblique (Figures 75, 91, 92). Anterior adductor muscle with anterior region about 3 times narrower than posterior region, divided transversally (dorsoventral) in two similar halves (quick and slow components). Posterior adductor muscle similar to, but inverted arrangement in comparison to anterior adductor muscle; components different, however, one of them horseshoe-shaped, occupying ventral and posterior sides (Figure 77); another component filling internal region of muscle, only exposed in posterior and dorsal sides (Figure 77). Pair of anterior foot retractor muscles long and narrow (Figure 80); originating just dorsal to anterior adductor muscle in area equivalent to 1/10 of adductor (Figures 75, 80); running ventrally and posteriorly; spreading after insertion in anterior and lateral regions of foot base. Pair of posterior foot retractor muscles similar to anterior pair, but about half narrower (Figures 75, 78, 80); originating just dorsal to posterior adductor muscle in area equivalent to 1/20 of that adductor; running ventral and anteriorly; inserting in posterior and lateral regions of foot base. Pair of palp muscles, septal and pallial muscles described below. Pair of foot protractor muscles absent.

FOOT AND BYSSUS (FIGURES 73, 74, 80): Foot conical, pointed; estimated volume equivalent to 1/6 of that of chamber of valves; base located in middle region of ventral surface of visceral sac. Byssal furrow shallow and very narrow, length about half of that of foot, offset ventrally and distally, lying along posterior surface and midline, ending at short distance from foot apex. Byssus found in a single specimen, brown, with single filament, narrow; proximal end attached to distal region of byssal furrow.

MANTLE (FIGURES 72–74): Dorsal fusion of mantle lobes about ⅓ of their edges, along entire hinge length and about ⅙ of valves height toward ventral, in both sides. Edges of mantle lobes with two folds. Inner fold fused between two lobes along entire posterior half (except for siphonal apertures) (Figure 74). Both lobes free from each other along anterior half, up to dorsal level of anterior adductor muscle; in this region both folds are of similar size, with height equivalent to 1/25 of valves height. Mantle edges thick, muscular, insertion relatively thick in pallial line (Figure 72, pm). Pallial muscles originating in pallial line in location about ⅓ from ventro-dorsal distance; no clear pallial sinus. Incurrent siphon as aperture of a septum formed by fusion of inner mantle edge folds; aperture about ⅕ of posterior fused region of mantle,



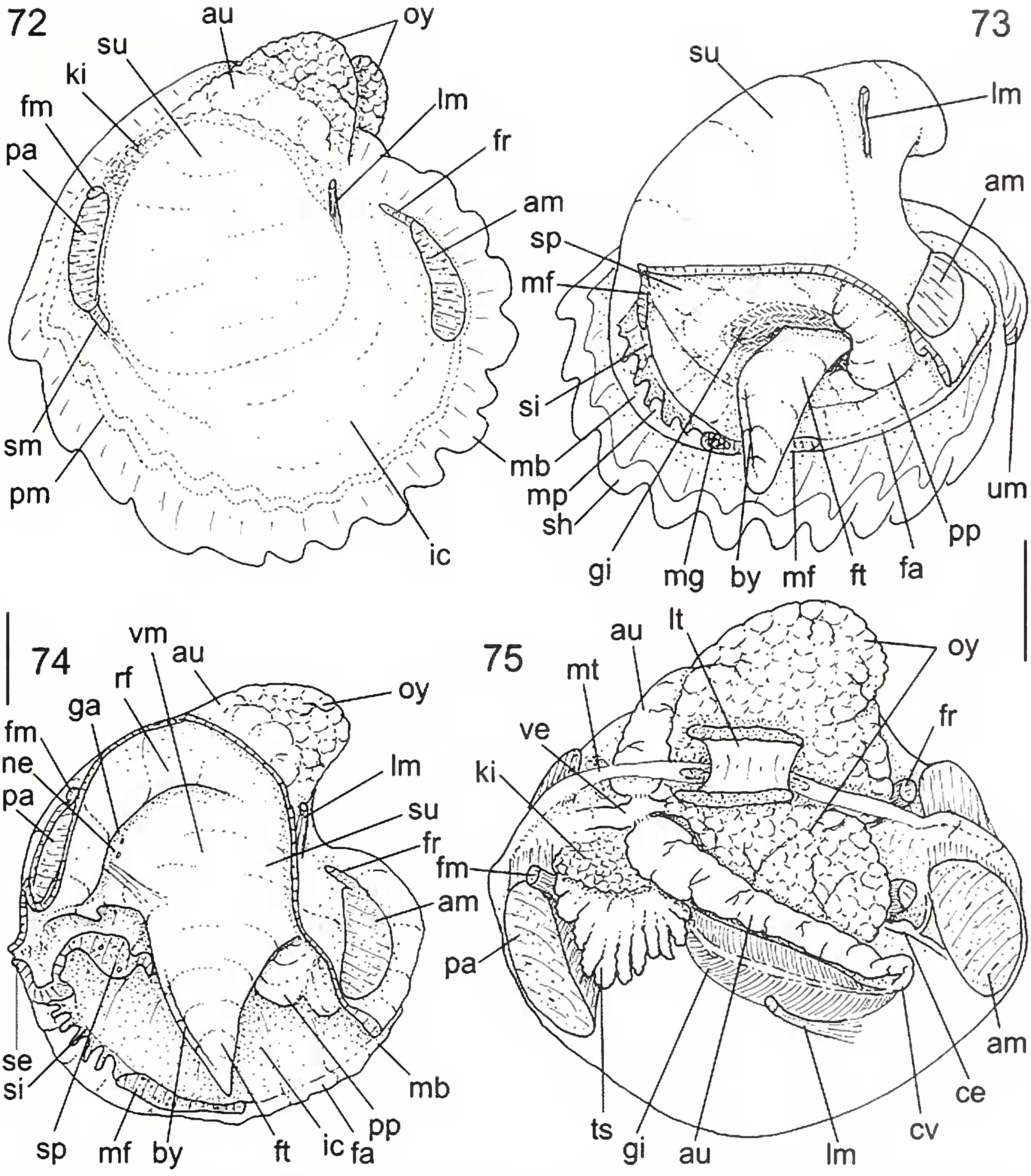
Figures 48–63. *Spinosipella* species. Shells. **48–54, 56–59.** *S. deshayesiana*, adult specimens. **48–53.** MNHN (Sta. CP1475, Fiji); 12.5 mm. **48.** Left valve, outer view. **49.** Right valve, outer view. **50.** Left valve, inner view. **51.** Right valve, inner view. **52.** Posterior view. **53.** Anterior view. **54.** Dorsal view, HGLC, from Philippines; 11.8 mm. **55.** *S. agnes* paratype, BMNH, 18.2 mm. **56–59.** Syntypes of *S. deshayesiana* MNHN. **56.** Outer view, specimen 1, left valve. **57.** Outer view, specimen 2 (possibly figured by Fischer, 1862a), right valve. **58.** Inner view, specimen 1. **59.** Inner view, specimen 2; length = 8 mm. **60–63.** *S. costeminens* Holotype MNHN. **60.** Outer view, left valve. **61.** Outer view, right valve. **62.** Inner view, left valve. **63.** Inner view, right valve; 17 mm.



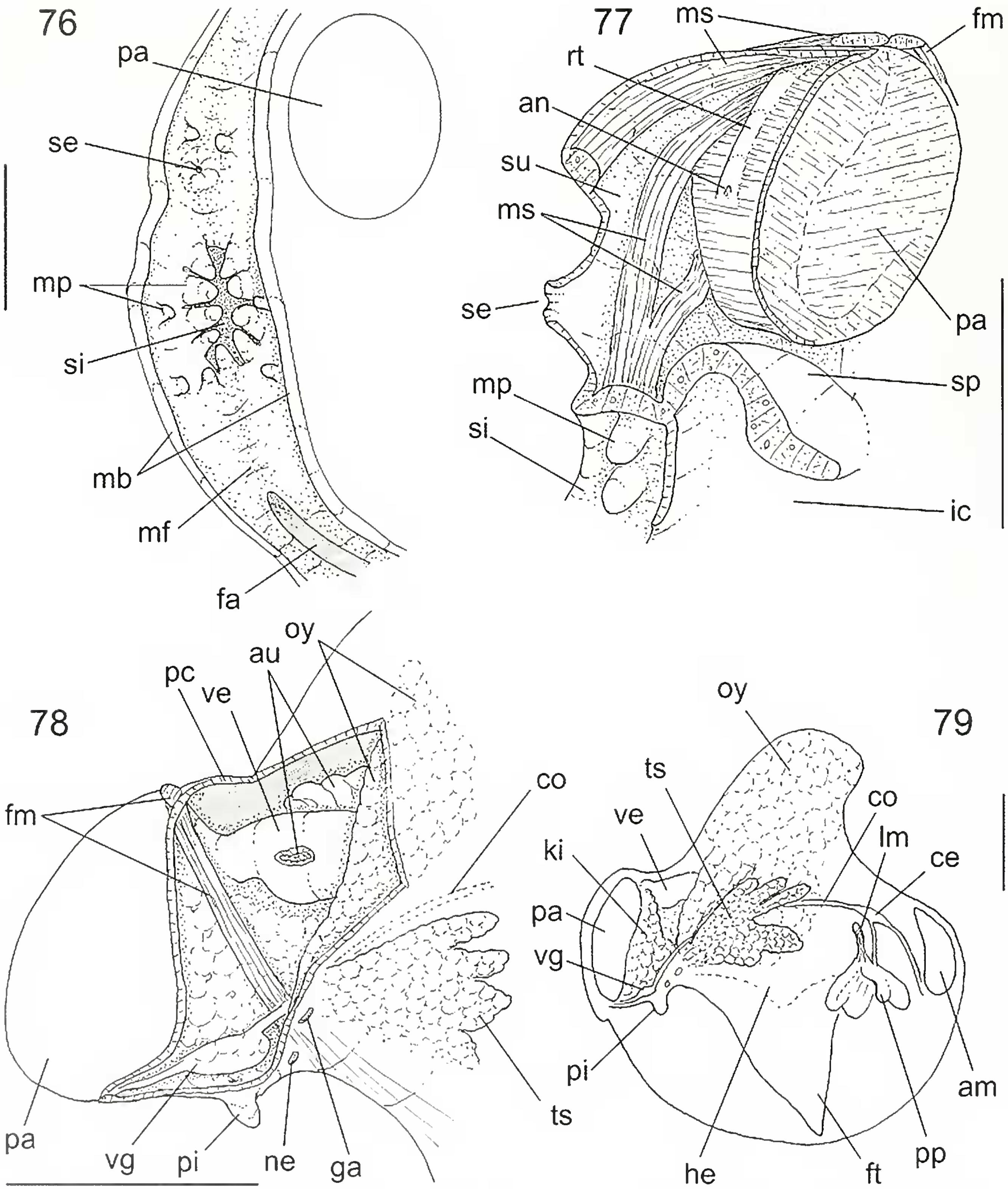
Figures 64–71. *Spinosipella* species. Shells. **64–65.** *S. costeminens* Holotype MNHN. **64.** Right valve, anterior view. **65.** Left valve, anterior view; 17.0 mm. **66–67.** *S. ericia* Holotype AMS, right valve. **66.** Outer view. **67.** Inner view; 5.8 mm. **68–71.** *S. costeminens* lacking projections on ribs, MNHN (Sta. CP 992, Vanuatu), right valve. **68.** Outer-right view. **69.** Anterior view. **70.** Posterior view. **71.** Inner view; 29.0 mm.

longer dorso-ventrally (Figure 76); walls thick, muscular; outer surface flanked by 9 tentacles surrounding siphonal aperture; all tentacles of similar size, turned inwards, somewhat conical, tip blunt and rounded, length equivalent to that of siphonal aperture; single unpaired tentacle located ventrally; five secondary smaller tentacles located externally, midway between siphonal aperture and mantle edge, of similar size, about ⅓ of size of major tentacles, well separated from each other, one of them located in ventral region of siphonal aperture, other four located laterally, in ventral half of siphon (Figure 76). Incurrent siphon a small pore located in small elevation, approximately midway between excurrent siphon and hinge; a pair of small tentacles similar to secondary tentacles of incurrent siphons, located laterally, in dorsal region of siphon base (Figures 74, 76, 77). Radial mantle gland present along mantle edges outer fold (Figures 73, 92, mg), occupying about half of outer fold volume, situated closer to inner surface of this fold.

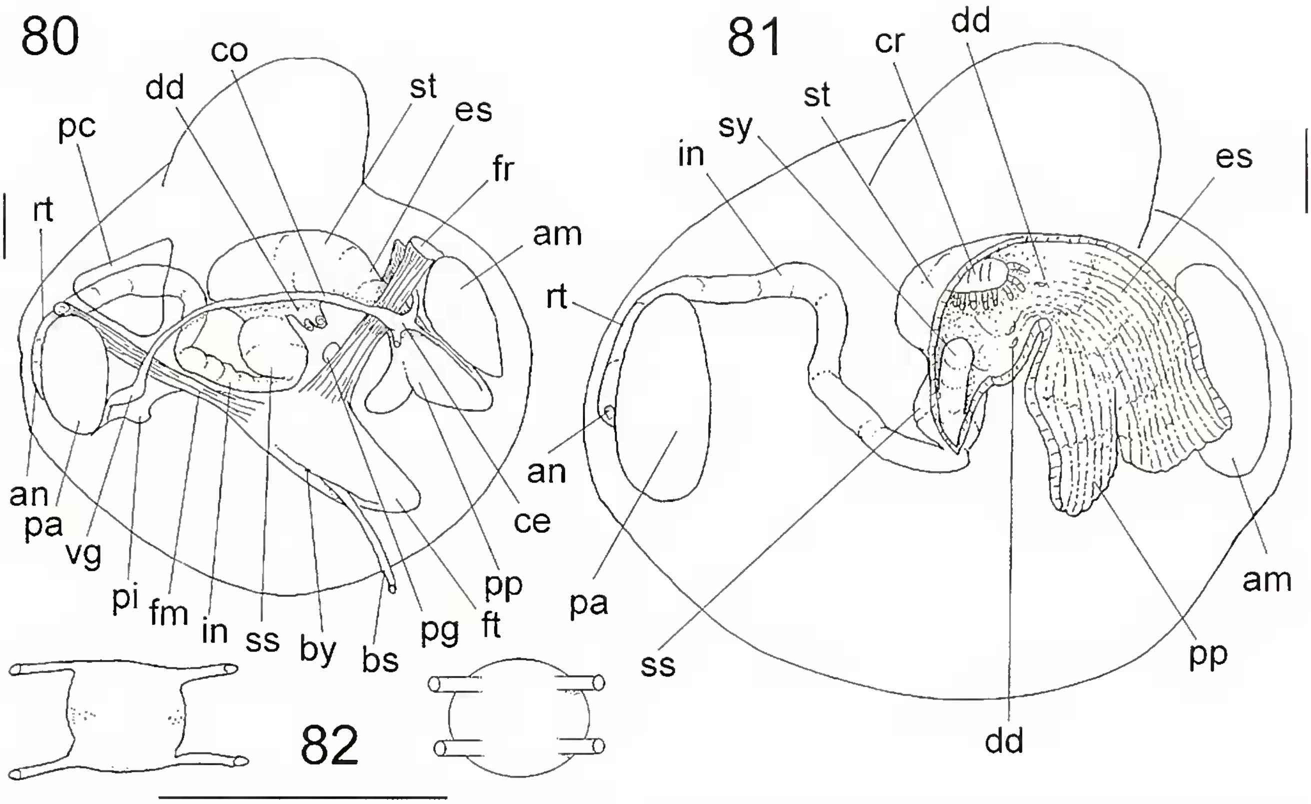
Pallial Cavity (Figures 73–75, 94, 95): Occupying about 70% of volume of valves. Transversal, horizontal septum located approximately midway in animal, i.e., supra- and infra-septal chambers of equivalent length (Figure 72). Paired palps low, wide, bilobed folds (Figures 73, 81, 95, pp) that occupy anterior third of dorsal surface of infra-septal chamber, permanently open as a funnel. Pair of palp muscles (Figures 72, 74, 79, lm) located laterally; originating in anterior region of umbonal cavity, in a distance from origin of anterior foot retractor equivalent to ⅓ of anterior adductor muscle height; located in same horizontal level of origin of anterior foot retractor; size equivalent to ¼ of that of anterior foot retractor; running ventrally attached to mantle for a distance equivalent to ⅙ of valve height; spreading after insertion in lateral region between inner and outer hemipalps. Palp muscles also connect anterior end of septum. Septum with two constituents: external one produced by a fold of mantle (about ⅔ of septum area); internal produced by gill (Figures 73, 95). External septum element thick, muscular; posterior muscles originating as a pair, just dorsal to posterior adductor muscle (Figure 77, ms); running ventrally immersed in mantle, at some distance from each other (equivalent to half of their width) and from midline, gradually becoming wider and thicker, in anterior surrounding posterior surface of posterior adductor muscle and lateral edges of excurrent siphon; some secondary muscular bundles originating from centroposterior region of posterior adductor muscle uniting with main, vertical bundles (Figure 77); muscles spreading within septum in region between incurrent and ex-



Figures 72–75. *Spinosipella deshayesiana*. Anatomy. **72.** Whole specimen just extracted from shell, right view. **73.** Same, right mantle lobe in its infra-septal region removed, right-slightly ventral view, left shell valve also shown. **74.** Same, right mantle lobe almost completely removed, right portion of septum also removed. **75.** whole specimen, dorsal-slightly right view, most of mantle and dorsal integument artificially shown as transparent, lithodesma (**lt**) shown in its *in situ* topology. Scale bars = 2 mm.



Figures 76–79. *Spinosipella deshayesiana*. Anatomy. **76.** Detail of region of siphons, posterior-slightly right view. **77.** Peri-anal chamber, right view, adjacent region of right mantle lobe sectioned and deflected to show inner surface and muscles, inferior region or right mantle lobe removed along median line. **78.** Reno-pericardial region and adjacent structures, right view, right wall of pericardium removed. **79.** Whole right view, showing topology of genital system, reno-pericardial structures, palps, main ganglia and muscles, most structures artificially shown as transparent. Scale bars = 2 mm.



Figures 80–82. *Spinosipella deshayesiana*. Anatomy. **80.** Whole right view, emphasizing digestive structures, main musculature and main nervous ganglia; topology of some adjacent structures also shown, everything else represented by transparency. **81.** Same, anterior region of digestive structures opened longitudinally, some objects inside stomach preserved, topology of some adjacent structures also shown. **82.** Visceral ganglia (left), ventral view, and pedal ganglia (right), postero-dorsal view. Scale bars = 1 mm.

current siphons. Outer component of septal muscles inserted in shell just ventral to posterior adductor muscle (Figure 72, sm), in area equivalent to 1/10 of that of adductor muscle insertion. Internal element of septum constituted by gills. Gill with both demibranchs narrow, of similar size, flattened, in same plane of remaining septum; both gills surrounding posterior and lateral regions of foot base (Figures 73, 75, 95). Gill attached to remaining septum via tissue; gill attachment to foot by cilia. Connection between gill filaments of 6–7 longitudinal, equidistant bridges of similar width of filaments. Papilla situated in posterior region of roof of supraseptal chamber (Figures 78–80, 94, pi), positioned just ventral to visceral ganglia, internally solid; length about 1/10 of posterior adductor muscle length and about 1/3 of it in width; tip broadly pointed, normally turned to anterior.

Visceral Mass (Figures 72, 75, 79): Strongly bilobed, as internal mould of well-separated umbos (Figures 72, 75). Most dorsal structures, just inside valve apexes, formed by sponge-like connective tissue. Pair of ovaries cream in color, occupying central and dorsal regions surrounding stomach and digestive diverticula, reaching dorsal areas up to dorsal sponge-like connective when fully developed. Testes brown, consistence harder, located ventrally and laterally, totally separated from ovaries; anterior region irregularly digitiform (Figures 75, 79, ts). Digestive diverticula situated compressed between stomach and gonads, color greenish-beige; occupying about 1/5 of visceral volume. Stomach and intestine lying in central region, occupying about 1/4 of visceral volume (Figures 80). Reno-pericardial structures located just anterior to posterior adductor muscle and posterior foot retractor muscles, with volume approximately 1/6 of visceral volume (Figures 75, 79).

Circulatory and Excretory Systems (Figures 75, 78): Pericardium located at short distance anterior to posterior adductor muscle; with about half of reno-pericardial volume, and with a pair of expansions toward anterior, surrounding roof of pallial cavity where lies pair of auricles. Auricles connecting to anterior end of gills, in short isolated ctenidial vein (Figure 75, cv); abruptly curving towards posterior and dorsal; after this curve, auricles increasing gradually, surrounding obliquely periphery of visceral mass in roof of pallial cavity (Figures 72, 75), walls thin, translucent; close to midline auricles abruptly narrowing and connecting to ventricle (Figures 75, 78); posterior region relatively lobed. Ventricle located in center of pericardium, surrounding intestine; relatively narrow. Kidney mostly solid, color dark purple-almost black; most of renal gland located just anterior to posterior adductor muscle, ventral to pericardium (Figures 75, ki); a pair of folds originating from this region, running long roof of pallial, supraseptal cavity, just ventral and external to auricles (Figures 74, rf), this pair of folds with about ⅕ of supraseptal chamber height, running posteriorly in middle region of roof of this chamber, gradually approaching visceral mass towards anterior, fusing to visceral mass after running about ⅙ of chamber length (Figure 74). Pair of nephropores as small slits located in posterior region of supraseptal chamber, covered by posterior end of renal fold, just dorsal to pair of posterior retractor muscles of foot (Figure 74, ne).

Digestive System (Figures 80, 81): Palps partially described above (pallial cavity), widely fused as pair of folds along midline (Figures 95, pp). Mouth central (Figure 95, mo), with sphincter relatively well developed. Esophagus with about ⅕ of visceral mass length, not attached to anterior adductor muscle, width about ⅓ of that of anterior adductor muscles; wall relatively thick, muscular; inner surface with about 20 longitudinal, narrow, low folds as continuation from those of palps (Figure 81). Stomach main chamber with about ¼ of visceral mass volume, elliptical, anteroposteriorly longer; walls thick, muscular (Figure 91, st). Gastric inner surface smooth; two pairs of ducts to digestive diverticula present, each one located in ventro-lateral region just posterior to esophageal insertion. Stomach normally containing 3–4 isopod crustaceans (Figure 81, cr). Style sac with about ⅓ of gastric main chamber volume, located in middle of gastric ventral wall, somewhat elliptical (longer dorso-ventrally); crystalline style occupying entire style sac (Figure 81, sy); inner surface of style sac smooth, lacking any fold separating it from intestine; gastric shield lacking. Intestine a single sigmoid loop with about half of style sac width. Inner surface simple, smooth. Intestinal portion crossing through pericardium in somewhat anteroposterior direction. Rectum attached to dorsal and posterior surface of posterior adductor muscle, with about ⅔ of remaining intestinal width. Anus simple, sessile, located in ventral third of posterior surface of posterior adductor muscle (Figure 77).

Genital System (Partially described above under Visceral Mass): Pair of testes and ovaries converging to a single common, short duct, of about 1/15 of visceral mass length. Genital pores small slits located at short distance from nephropores (Figures 74, 78, 94, ga).

Central Nervous System (Figures 80, 82): Cerebral ganglia somewhat triangular, each ganglion with volume equivalent to 1/15 of that of anterior adductor muscle; anterior end narrow, possessing thick pair of nerves running to pallial region dorsal to palps; pair of ventral nerves also thick, originated in middle region of ganglia, running ventrally to palps; Posterior end originating cerebro-visceral connective (Figures 80, 106); cerebral commissure length about ⅓ of posterior surface of anterior adductor muscle. Pair of cerebro-visceral commissures relatively thick, running though visceral mass between stomach and testes. Pair of pedal ganglia located in ventral third of anterior pair of pedal retractor muscles, touching these muscles, both totally fused with each other along midline, almost forming a sphere, volume of both equivalent to that of each cerebral ganglion; pedal nerves and cerebropedal connectives originating subterminally in posterior surface of ganglia. Pair of visceral ganglia located anterior to ventral surface of posterior adductor muscle; both also totally fused with each other along median line, being somewhat squared in ventral view; size equivalent to that of pedal pair of ganglia; cerebrovisceral connectives and siphonal nerves located in vertices.

Measurements (respectively length, height, width, in mm): HGLC: 11.5 by 12.2 by 12.0; MNHN (Sta. DW11): 15.7 by 17.7 by 9.2 (valve); MNHN (Sta. CP889): 19.7 by 17.0 by 9.1 (valve).

Geographic Distribution: South and Central Indo-Pacific in 146–805 m depth.

Material Examined: Paratypes of *S. cricia*: AUSTRALIA; South Cape Wiles, 174–183 m, 35°39′ S, 136°40′ E, AMS 032068, 1 left, 1 right valves (Zoological Results of the F.I.S. Endeavour, 28 Aug. 1909).

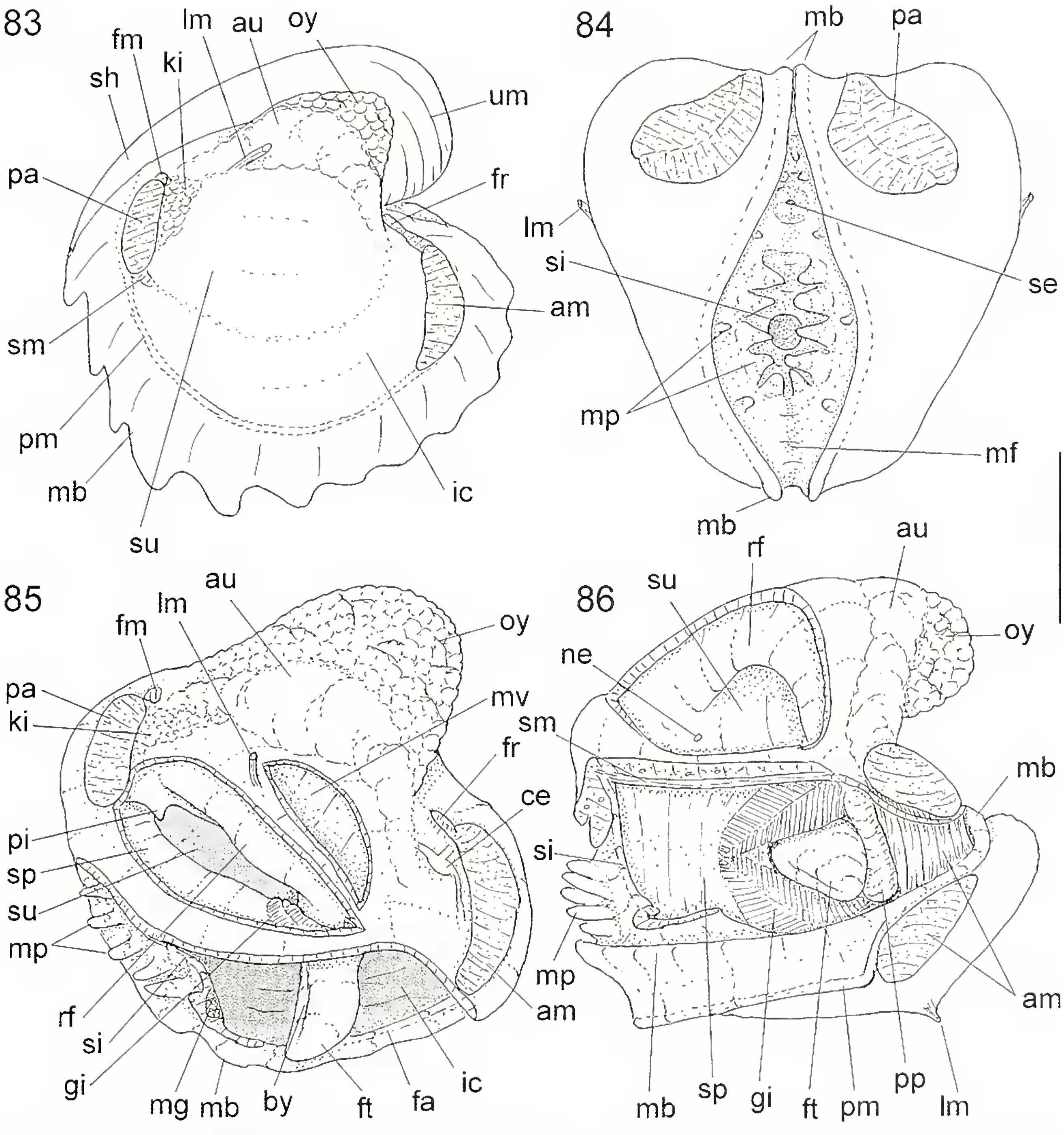
Other Material Examined: Holotype of *S. japonica*: JAPAN. ANSP 49639, 1 shell. MNHN. SW PACIFIC. Loyaute Islands, 16 lots [122 v]. TONGA IS. 12 lots [59 v]. GUAM. Marianas Islands, 3 lots [15 v]. AUSTRALIA. South Cape Wiles, 1 lot [6 v]. NEW CALEDONIA. South, 3 lots [7 specimens]; Banc Esponge, 2 lots [3 specimens]; Chesterfield Plateau, 1 specimen. PHILIPPINES. Aliguri Is. 2 lots [1 specimen and 3 v]; Bohol Sea, Off Balicasag Island, 1 lot [1 v]. FIJI. 1 specimen. MYANMAR (BURMA). 1 lot [5 v] Preparis North Channel, 1 lot [4 v]; N.W. of Tavoy I., 1 lot [11 v]. ANDAMANS SEA. 1 lot [1 v]. THAILAND. Phuket I., 1 lot [11 v]; Andaman Sea, 1 lot [1 v] (Details in Simone and Cunha, in press.)

Spinosipella costeminens (Poutiers, 1981)
(Figures 60–65, 68–71, 83–92, 103–108)

Verticordia (Spinosipella) costeminens Poutiers, 1981: 351 (pl. 4, figs 1–4, text fig 5).
Spinosipella costeminens.—Poutiers and Bernard, 1995: 110, 143, 158 (figs. 1–2).

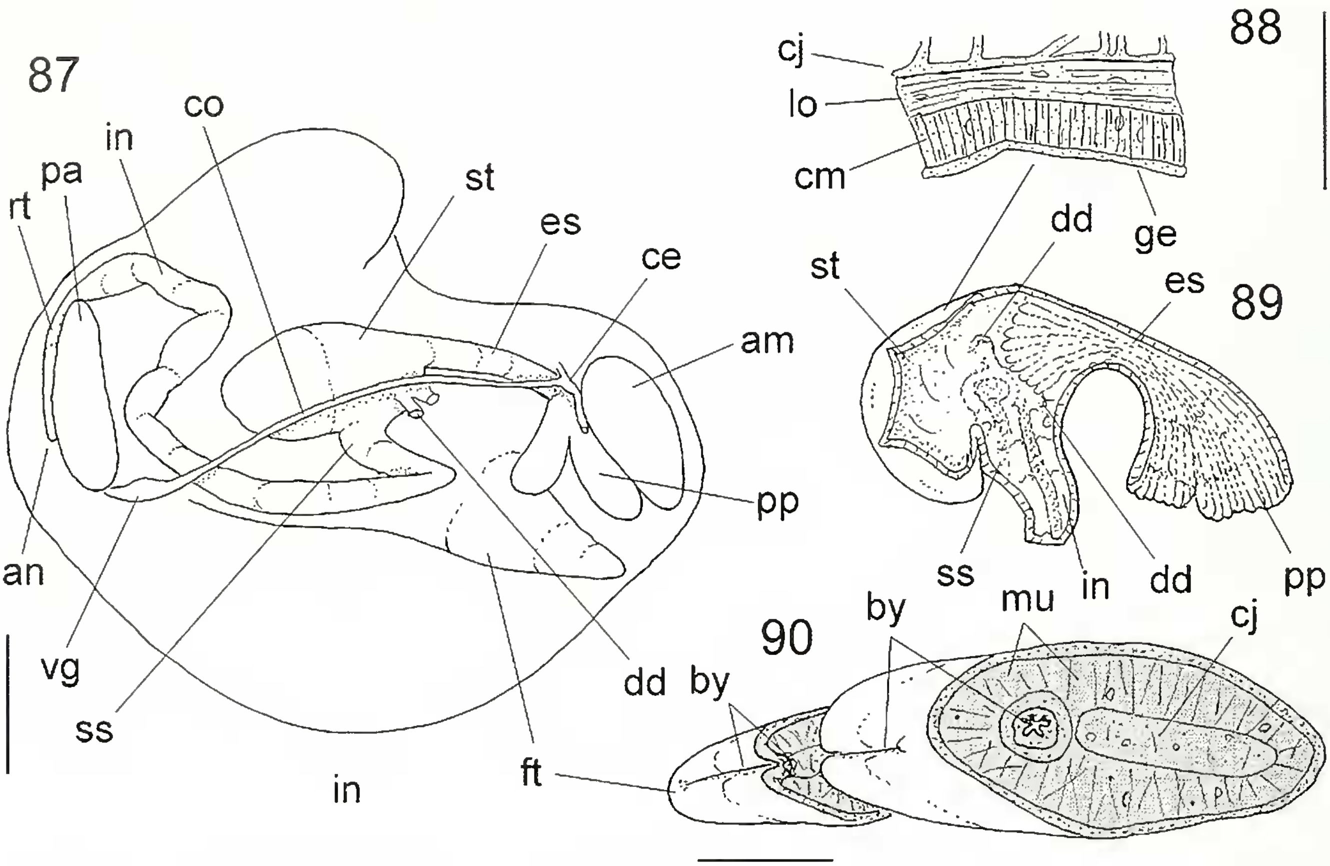
Diagnosis: Shell with 16–17 tall radial ribs, those more posterior to middle surface very taller, normally possessing blade-like projections along tip; 3–4 more posterior abruptly lower, preceded by a very tall, carina-like rib.

Description: Shell: Up to 30 mm. Color white. Degree of convexity (width/length) in each valve approximately 0.50. Outer surface prickly, with somewhat chaotic organization (Figures 60, 61, 68–70). Sculptured by strong, uniform, arched, radial ribs, from 16 to 17 in each valve (Figures 60, 61); ribs increasing from region anterior to umbo to region between middle and posterior thirds, last ribs in this region taller and more separated from each other, last one on a weak carina (Figure 70); larger ribs normally possessing blade-like, projection



Figures 83–86. *Spinosipella costeminens*. Anatomy. **83.** Whole specimen with right valve extracted, right view. **84.** Specimen extracted from shell, posterior view, showing siphonal area. **85.** Whole right view, some portions of right mantle lobe extracted, particularly regions ventral to septum, and ventral and dorsal to renal fold (**rf**) to expose inner surface; cerebral ganglion (ce) seen by transparency. **86.** Same, ventral-slightly right view. Scale bar = 5 mm.

along tip; posterior third as a slope, having 3–4 ribs similar to those of anterior region; blade like projection absent in some specimens (Figures 68–71). Posterior edge about twice broader than anterior edge. Between umbos and anterior edge a concavity bearing transversal ribs similar to ribs of remaining region (Figures 64, 65); preumbonal region narrow, smooth about 10% of shell length (Figures 64, 65, 69). Anterior, ventral, and posterior edges forming zigzag (Figures 62, 63, 71, 103), with tips longer and narrower projected in those middle and larger ribs. Hinge with a large cardinal tooth in right valve, stubby, tall (about 10% of valve width), broadly



Figures 87–90. *Spinosipella costeminens*. Anatomy. **87.** Whole right view, mainly showing digestive tubes and main ganglia, topology of some structures also shown. Scale bar = 5 mm. **88.** Scheme of layers of tissue in indicated region of stomach. Scale bar = 0.5 mm. **89.** Fore- and midgut opened longitudinally for exposing inner surface (same scale of Figure 87). **90.** Foot, ventral-slightly posterior view, sectioned transversally in two levels to show inner layer of tissues. Scale bar = 1 mm.

pointed, somewhat flat (Figures 63, 71, 103); correspondent socket in left valve shallow, restrict to dorsal surface; this socket flanked by small posterior tooth, with insertion of anterior valve edge approximately in middle region of this tooth (Figure 62), anterior tooth absent (Figure 62).

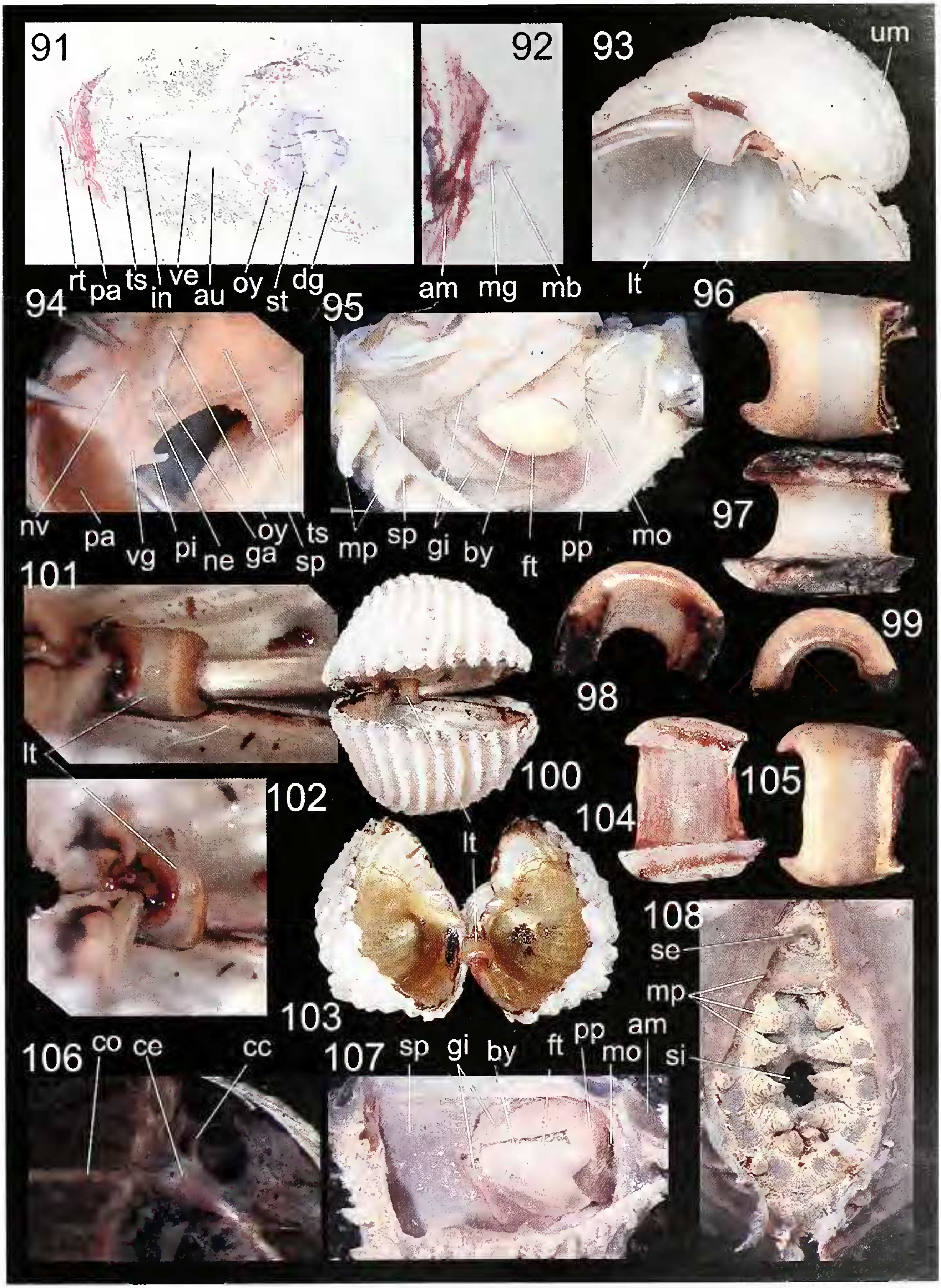
Additional details for this species see Poutiers (1981), Poutiers and Bernard (1995).

Lithodesma (Figures 103–105): Characters similar to those in preceding species, differing in being proportionally shorter and wider (Figures 104–105). Length about ⅕ to ⅙ of hinge length, and about 1.5 times wider and long.

Main Muscle System (Figures 83–87): Characters similar to those in preceding species. Anterior adductor muscle about 20% dorso-ventrally longer (Figures 83, 85).

Foot and Byssus (Figures 85, 84, 90, 107): Shape and disposition similar to those in *S. deshayesiana*. Byssal gland relatively deep, running immersed in ventral region of pedal musculature at about half of byssal furrow

Figures 91–108. *Spinosipella* species. Anatomy. **91.** *S. costeminens*, middle horizontal, longitudinal section through visceral mass at same level as pericardium (MNHN sta. CP767, Mallory, 5 μm). Scale bar = 2 mm. **92.** Same, detail of posterior region of mantle border. Scale bar = 1 mm. **93–102.** *S. deshayesiana*. **93.** Detail of hinge region of left valve with lithodesma (**lt**) still attached, right view. Scale bar = 2 mm. **94.** Detail of posterior region of supraseptal chamber, right view, right mantle lobe removed (MNHN sta. DW1499). Scale bar = 1mm. **95.** Infraseptal chamber roof, ventral view, right mantle lobe removed (MNHN sta. CP767). Scale bar = 2 mm. **96–99.** Lithodesma (MNHN sta. DW739). Scale bar = 1 mm. **96.** Ventral view. **97.** Dorsal view. **98.** Posterior-slightly dorsal view. **99.** Posterior view. **100.** Same specimen, empty shell, ventral view, valves slightly open, lithodesma still in situ. Scale bar = 2 mm. **101.** Same, detail of hinge and lithodesma. **102.** Same, ventral-slightly anterior view. **103–108.** *S. costeminens*. **103.** Shell, ventral view, valves open, lithodesma still attached to left valve (MNHN sta. CP1460). Scale bar = 2 mm. **104–105.** Lithodesma, same lot (other specimen), dorsal and ventral views respectively. Scale bar = 1 mm. **106.** Detail of anterior region, right view, integument removed, mainly showing right cerebral ganglion (**ce**) (same lot). Scale bar = 1 mm. **107.** Infraseptal chamber roof, ventral view, right mantle lobe removed (MNHN CP767). Scale bar = 1 mm. **108.** Detail of posterior (siphonal) region, posterior view (MNHN CP1460). Scale bar = 2 mm.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length towards dorsal (Figure 90, bv). Thick muscular layer surrounding a nucleus of conective tissue (Figure 90, cj).

Mantle (Figures 84–86, 92, 108): Characters similar to those in preceding species, with following distinctive characters. Pair of secondary tentacles positioned between incurrent and excurrent siphons (Figures 84, 108); remaining tentacles similar in size and position. Ventral pair of tentacles of incurrent siphon generally symmetrical. Zigzag formed by mantle edge having secondary folds positioned in more distal tips, possibly elated to taller radial shell ribs (Figure 108). Radial mantle gland (Figure 92) similar to *S. deshayesiana*.

Pallial Cavity (Figures 85–86, 107): Characters similar to those in preceding species, except for wider platform between posterior region of gills as part of septum (Figure 107).

Visceral Mass (Figures 85–87): Characters similar to those in preceding species, differing mainly by wider region separating pair of renal folds in supraseptal chamber (Figure 85).

Circulatory and Excretory Systems (Figures 85, 91): Pericardium and heart with characters similar to those in *S. deshayesiana* (Figure 91). Kidneys of similar features, differing mainly by enlargement of pair of renal folds (Figures 85–86, rf), taller and wider, almost dividing supraseptal chamber in two—internal and external—halves. Height of renal fold about 80% of that of supraseptal chamber height. In addition to an enlargement, both renal folds still have posterior end in more anterior position and wider separation between folds and visceral mass (Figure 85).

Digestive System (Figures 87–89): Characters similar to those in preceding species. Esophagus with about ⅓ of visceral mass length, running horizontally, perpendicular to posterior surface of anterior adductor muscle (Figure 87, es). Stomach main chamber with longer region as a blind-sac projected posteriorly. Gastric wall constituted by external layer of weak connective tissue (Figure 88, cj), two thick muscular layers of similar size, with outer layer of longitudinal muscle and inner layer of circular muscle (Figure 88, lo and cm). Inner surface of stomach (Figure 89) with posterior end of esophageal folds clearly more evident that together form a flat fold. Another ventral fold surrounding apertures to digestive diverticula. Gastric style narrower (about ⅙ of gastric width); internally a pair of tall folds separating intestinal from style sac components (Figure 88, ss, in).

Genital System: Characters similar to those in preceding species. Separated masculine and feminine components of gonad shown through histological sections in Figures 91(ts, ov).

Central Nervous System (Figures 87, 106): Three ganglia with similar localization and size to those of preceding species.

Measurements (respectively length, height, width in mm): MNHN (Sta. 1361): 22.0 by 28.1 by 12.5 (valve); MNHN (Sta. CC996): 20.0 by 24.3 by 14.3 (valve); MNHN (Sta. CP992): 19.6 by 23.3 by 12.6 (valve).

Geographic Distribution: Tropical West Pacific.

Depth Range: 750–925 m.

Material Examined: Holotype; Additional material (MNHN): SW PACIFIC. 4 lots [32 v, 11 specimens]; Wallis Is., 6 lots [15 v]; Banc Combe, 5 Lots [28 v]; Fortuna Is., 5 lots [18 v]; Banc Waterwitch, 2 lots [3 v]; Banc Tuscarora, 29 lots [63 v]; South Vanuatu - Monts Gemini, 4 lots [4 v, 1 specimen]; TONGA IS. 8 lots [52 v]; Eua Is. 6 lots [12 v]; Seamount, 6 lots [29 v]; South of Nomuka group, 1 lot [25 v]; Ha'apai Group, 2 lots [4 v]; N Ha'apai group, 3 lots [6 v]; NW Tongatapu, 3 lots [16 v]; SW Tongatapu, 5 lots [22 v]; Tongatapu, 6 lots [8 v]; S. Nomuka group, 2 lots [6 v]; Vava' group, 1 lot [2 v]; NEW CALEDONIA. 5 lots [5 v, 5 specimens]; Lord Howe, 1 lot [1 v]; Banc Nova, 2 lot [8 v, 1 specimen]; North New Caledonia, 10 lots [tota 20 v]; South New

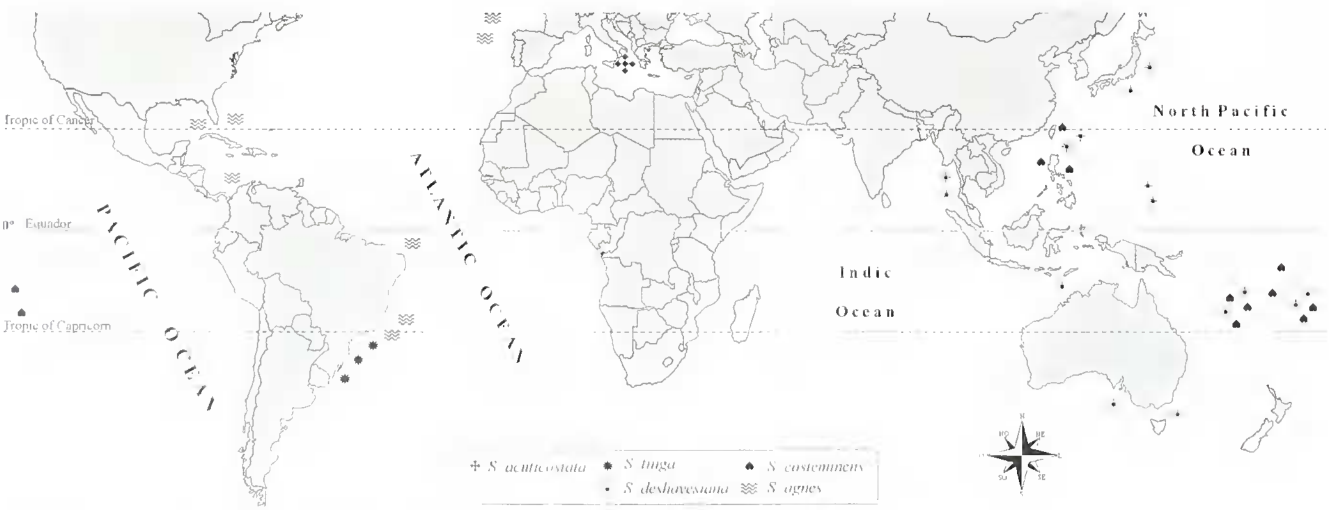

Figure 109. Geographic distribution of *Spinosipella* spp.

Caledonia, 13 lots [46 v, 1 specimen]; off Norfolk, 18 lots [98 v]; Banc Esponge, 11 lots [144 v]; Banc Kaimon-Maru, 9 lots [38 v]; Banc Antigonia, 1 lot [1 v]; Banc Jumeau-West, 4 lots [17 v]; Banc Introuvable, 7 lots [16 v]; Banc Stylaster, 1 lot [1 v] ; Volcans Hunter and Matthew, 2 lots [2 v]; S.E. New Caledonia, 2 lots [2 v]; East New Caledonia, 6 lots [30 v] Banc Capel, 1 lot [lota 12 v]; Banc Kelso, 1 lot [6 v]; I. Loyaute, 22 lots [44 v]. FIJI. South of Viti Levu, 42 lots [328 v]; Southeast of Viti Levu, 17 lots [57 v]; Bohol/Sulu Seas, 2 lots [5 v]; Bohol Sea - Balicasag Island, 3 lots [5 v]; Bordau, 1 specimen; TAIWAN. Bashi channel, 2 lots [3 v]; South China Sea, 1 lot [2 v]; East Taiwan, 2 lots [5 v]. (Details in Simone and Cunha, in press.)

DISCUSSION

The Genus *Spinosipella* Within the Verticordiidae. Despite their larger size, the prickly outer surface of the shell, and the reduction of the lunule, which differentiates *Spinosipella* from the remaining verticordiids, this taxon has traditionally been considered a subgenus of the genus *Verticordia*. This set of characters is sufficient in my opinion to allocate *Spinosipella* as a separate genus. This view was previously defended by the author of the genus (Iredale, 1930) and by Poutiers and Bernard (1995). Other distinctive characters are the spiral umbones (Figures 5, 7, 21, 22, 33, 54, 53), the tall, somewhat uniform radial sculpture, triangular in section; and the obesity of the valves. The spiral umbones and the obesity of *Spinosipella* are quite similar to those in the fossil genus *Pecchiolia* Savi and Meneghini in Murchison, 1850 [type-species (by monotypy): *Pecchiolia argentea* Savi and Meneghini in Murchison, 1850 (= *Chama arictina* Brocchi, 1814) middle Tertiary, Europe] (Keen, 1969: 857), from which *Spinosipella* differs in having well-developed ribs and zigzag edges.

The full genus status of *Spinosipella* is based on the differences with the typical *Verticordia* sensu stricto [type species (by monotypy) *Verticordia cardiiformis* Sowerby, 1844], such as the higher size and obesity of the valves; the additional development of the prickly surface (which also covers the radial ribs, whereas in *Verticordia*, when a prickly surface is present, it does not cover the radial ribs), the absence of lunule; the spiral fashion of both valves; and the similarity among the radial ribs (representatives of *Verticordia* usually have an unusually larger rib or space between ribs). The same set of characters also differentiates *Spinosipella* from *Trigonulina* d'Orbigny, 1842 [type species (by monotypy) *T. ornata* d'Orbigny, 1842] in the sense of Jung (1996: 46–47).

Representatives of *Spinosipella* also resemble those of the genera *Haliris* Dall, 1886, and *Euciroa* Dall, 1881, by their larger size, convexity, and prickly shell surface. *Spinosipella* differs from those two genera, however, in the higher degree of convexity, reflected in more obese shells in its species; in the much more developed and taller radial ribs; higher degree of spiralization of the valves; and in the expansion of the ribs beyond the shell margin.

Further analysis on the verticordiid systematics and phylogeny can be found in the literature (e.g., Pelseneer, 1888; Salvini-Plawén and Haszprunar, 1982; Bieler and Mikkelsen, 1992).

COMPARISON BETWEEN THE *SPINOSIPELLA* SPECIES

The differentiation between the five species of *Spinosipella* is summarized in the respective diagnoses and in Table 1. The degree of differentiation in the samples of each species examined allows for specific separations. The number of radial ribs is the most notable feature; despite certain a small amount of intraspecific variation, the number of radial ribs is somewhat constant in each species, at least in specimens of larger size. The fossil *S. acuticostata* is the species with fewest ribs, 12–13 (Figures 36, 38, 39), while *S. deshayesiana* has the largest number of ribs, 16–19 (Figures 46, 48, 49, 54, 53). The other species possess an intermediary number of ribs. The species of *Spinosipella* usually have radial ribs of relatively uniform size; the single exception is *S. costeminens*, which has ribs clearly increasing posteriorly; in the posterior shell slope, however, the ribs abruptly reduce in size, although in some specimens, particularly in the young ones, this character is not so clear, i.e., the ribs are somewhat uniform-sized. The shell inflation is well developed in most *Spinosipella* species, but this is clearer in

Table 1. Comparison of characters between the five studied species of *Spinosipella*.

Character	*Spinosipella acuticostata*	*Spinosipella agnes*	*Spinosipella tinga*	*Spinosipella deshayesiana*	*Spinosipella costeminens*
Distribution	Mediterranean	Tropical W. Atlantic; Caribbean; to SE Brazil	S-SE Brazil	South and Central Indo-Pacific	Tropical West Pacific
Shell Inflated	Strongly	Highly	Weakly	Strongly	Highly
Sculptured between radial ribs	Radial	Disorganized	Radial	Radial	Disorganized
Prickly ribs outer surface	Rough	Rough	Weakly prickly	Strongly prickly	Rough
Number of Ribs	12–13	15–17	17–18	18–19	16–17
Size (mm)	20.0	20.2	10.4	11.5	20.0

the larger specimens; while the young specimens are considerably flatter (Figures 41–45). The prickly outer shell surface is an outstanding character of the *Spinosipella* species; however, this character is conservative among the five species; the single exception is the relatively chaotic arrangement in *S. agnes* (Figure 8) and *S. costeminens*, while in the remaining species a radial arrangement is apparent (parallel to the radial ribs) (Figure 32). The Pacific species *S. deshayesiana* has much larger, crispy prickles along the tip of the ribs (Figures 42, 45, 46, 48, 49). This is lacking in the remaining species, except in some very young specimens (e.g., USNM 810889, *S. agnes*, 6 mm), where the prickles, however, are not fully developed. The prickly surface is strongly damaged in eroded specimens (Figure 55), becoming almost completely smooth. *Spinosipella deshayesiana*, perhaps because of this character, has the distal tips of the zigzag edges of the shell even longer and more projected (Figures 41, 44, 47, 50, 51, 59, 67). The series of radial ribs is interrupted in the region between the umbos, where a triangular smooth area appears. This area is particularly large in *S. agnes* (Figures 7, 9), but is practically absent in *S. tinga* (Figures 21, 22); it is narrow in the remaining three species. The size of the specimens appears to be another distinctive feature, as *S. tinga* is small (around 10 mm), whereas the remaining species are larger (20–30 mm). The hinge does not vary much between the *Spinosipella* species; however, some particularities exist. The posterior tooth of the left valve is well developed in *S. agnes* [Figures 4, 10, 12, 27, 28 (arrow)], very low in *S. acuticostata* (Figures 35, 39), and practically absent in remaining species (Figures 20, 25, 50). The tall and pointed cardinal tooth of the right valve is more developed in *S. agnes*, in such it is also sharply pointed and curved (Figures 3, 10, 12). In the remaining species this tooth is weakly shorter and more rounded (Figures 26, 34, 47, 51).

The geographic and stratigraphic distribution are somewhat mutually exclusive for most of the species (Fig. 72); *Spinosipella acuticostata* is the only Mediterranean species, *S. agnes* occurs from Florida to Rio de Janeiro, *S. tinga* is found from Rio de Janeiro to Rio Grande do Sul, along the Brazilian coast. The fine-resolution distribution of the Indo-Pacific species is still unclear, but *S. deshayesiana* and *S. costeminens*, appear to be sympatric. *Spinosipella acuticostata* is a fossil species, occurring in Pliocene strata, while the remaining species are found in the Recent. Apparently no Recent *Spinosipella* occur in the Mediterranean.

All samples of *Spinosipella* from the Atlantic and Mediterranean have previously been accepted as belonging to the single species *S. acuticostata* (e.g., Abbott, 1974; Abbott and Dance, 1983; Rios, 1994). However, analyses of the conchological, geographic, and stratigraphic differences, show that the separation into three species is warranted. As the shape changes considerably during ontogeny, a specimen of *S. agnes* at same size as the holotype of *S. tinga* was chosen to show the differences between those species. Figures 28–31 illustrate these differences. *Spinosipella agnes* has fewer, taller, and more widely spaced ribs than *S. tinga* (Figures 19, 29). The shape of the shell edge is much more uniform in *S. tinga* than in *S. agnes*, in that the tips of the ribs are more expanded, extending longer beyond the shell margin (Figures 20, 24, 28). The posterior cardinal tooth in the hinge of the left valve is present in *S. agnes*, in animals larger than 5–6 mm, while this tooth is never present in *S. tinga* (Figures 20, 25, 27–28, arrow). The degree of convexity is higher in *S. agnes* and in *S. tinga* (Figures 30, 31); *S. agnes* has a degree of convexity (width/length) in each valve of about 0.57, while *S. tinga* it is 0.47.

The comparison of the previously valid species *Spinosipella ericia*, including paratypes (Figures 41–44), and *S. deshayesiana*, does not reveal any distinction between them. Normally, specimens of smaller size were identified as *S. ericia*, and the large ones as *S. deshayesiana*. But examination of shell features along a growth series show a complete gradient linking the two taxa. The same lack of distinction is found in the literature for both species, including the original descriptions. For these reasons, despite the fact that *S. ericia* is the type species of the genus, the older name *S. deshayesiana* should be used. Furthermore, a type specimen of *S. japonica* was also examined (Figure 45), confirming the synonymy of this species with *S. deshayesiana*.

The distinction between the Pacific species *Spinosipella deshayesiana* and *S. costeminens* is not always easy. With the large quantity of specimens kindly provided by the MNHN (Paris), it was possible to analyze the degree of variation of both species. *Spinosipella costeminens* mostly has samples with shell possessing the outstandingly large, carina-like spiral ridge between the middle and posterior thirds of the shell, but sometimes this ridge is not so different from the others, and the animal become more rounded, similar to *S. deshayesiana*. The distinction is based mainly on the presence of at least a weak carina in the region between middle and posterior thirds, and also by the more robust ridges of *S. costeminens* specimens (Figures 60, 61), while those of *S. deshayesiana* lack any clear radial carina and the ridges are more delicate, uniform and apparently close from each other (Figures 46, 48).

The lot USNM 63200 includes 3 valves (2 left and 1 right), collected in Barbados, the known geographic distribution of *Spinosipella agnes*. However, the right valve has the characters of *S. deshayesiana*, instead of those of *S. agnes*. In addition, is looks different in the state of conservation, color and associated sediment, from the other 2 valves of the same sample.

DISCUSSION ON ANATOMY

More in-depth anatomical descriptions and discussions on verticordiids are provided by Allen and Turner

(1974), who studied 19 species of several genera. However, no information on the anatomy of the genus *Spinosipella* is found in the literature. Although anatomical information is available here only for two of the five species of the genus (of course one of them is a Pliocene fossil), some systematic inferences can be made based on the scenario given in the literature the Verticordiidae and related families (Allen and Turner, 1974, and others, e.g., Fisher, 1860, 1862b; Pelseneer, 1888; Nakazima, 1967; Allen and Morgan, 1981). Besides the conchological characters discussed above, some anatomical features are possibly restricted to *Spinosipella*, such as: the wide lithodesma (Figures 93, 96–104, lt); the simplified siphonal tentacles (Figure 108), which normally have secondary papillae; the papilla on the roof of the excurrent chamber (Figures 78–80, 85, 94: pi); the absence of incurrent valve in infraseptal chamber. However, wide lithodesma have been reported for *Policordia lisbetae* Knudsen, 1970 (fig. 90), which has very different shell and pallial tentacular characters. The study on the incurrent siphonal structures is of particular importance in septibranchs, as the modified incurrent siphon is the main structure used in prey capture (Morton, 1987).

On the other hand, some features appear to be characteristic of Verticordiidae, such as: elongation of lateral region of kidneys; the muscular stomach (see also Purchon, 1956, 1963); the separation between testis and ovary. By the proximity of the esophagus from anterior adductor muscle, by the lack of incurrent valve, and by the simplified buccal structures, e.g., lack of buccal cavity and tongue, it is possible to suggest that *Spinosipella* is a basal taxon inside Verticordiidae. Unfortunately, no member of the genus was analyzed in the recent comparative studies on anomalodesmatans (Harper et al, 2006).

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